Frontispiece : Sitka spruce clone 8014. Fourth stage of flushing - needles visible through thin bud scales at side of bud.

Temperature effects on the vegetative growth cycle of Sitka spruce (*Picea sitchensis* (Bong.) Carr.)

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1978.

I hereby declare that this thesis has been composed by myself from the results of my own work.

Signed: [redacted]

Date: 7th April, 1978.

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PREFACE

This study was conducted jointly with the Physiology section of the Forestry Commission Research Division, utilising the growth room facilities and the nursery at their Northern Research Station, Bush, Midlothian. I gratefully acknowledge the use of these facilities and the abundant supply of plants made available to me.

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SUMMARY.

The aim of this study was to elucidate the role of temperature as an influence on the vegetative growth phases of Sitka spruce (Picea sitchensis (Bong.) Carr.) and the results indicate that temperature plays a major part in controlling the alternating periods of growth and dormancy.

Flushing in Sitka spruce is a response to warm temperatures and was considerably retarded at low temperature. Extension growth was optimal for most of the plant types tested with a day/night temperature differential of 12°C, with a day temperature of 20°C. Current temperatures affected the morphology of the plants - low temperature restricted the elongation of stem units and reduced needle extension. Different genotypes reacted differently to temperature as did different provenances, and temperature affected both rate and duration of growth.

The latitudinal trend of growth cessation with decreasing daylength is confirmed, but the involvement of temperature in this response is also demonstrated. Low temperatures upset the latitudinal trend, while warm temperatures shorten the critical daylength. Southern provenances are more flexible in their response to temperature than northern provenances.

Bud development is enhanced by warm temperatures, while buds matured at low temperatures tended to flush earlier the following year. This result indicates a

deeper dormancy of buds matured in warm temperatures.

The chilling requirements of Sitka spruce provenances are satisfied by six to eight weeks at a temperature $\leqslant 6^{o}C$. No provenance trend in chilling requirement was found and chilling period was not related to subsequent extension growth. Insufficient chilling led to irregular flushing.

In the field the utilisation of a short part of the frost-free season for growth was demonstrated and the main environmental factors affecting the weekly extension growth of the four-year old trees were solar radiation, photoperiod and rainfall.

CHAPTER 1. INTRODUCTION.

Many studies have investigated the effects of temperature and photoperiod on the growth of a range of tree species and it is well known that temperature and daylength are among the more important factors controlling the yearly alternation of active growth and dormancy in forest trees.

Sitka spruce (Picea sitchensis (Bong.) Carr.), a species which plays an important role in British forestry, has until recently been relatively neglected in physiological research and in particular little detailed study has been made of the effects of temperature on the vegetative cycle. A native of the west coast of North America, the natural distribution of Sitka spruce extends from Alaska to California, mainly restricted to the 'fog belt'. As a result of this long latitudinal range, temperature dispersion and gradation in length of growth period are seen within the distribution.

The annual cycle of development reflects the genetic adaptation of trees to the annual climatic cycle of the habitat. Provenance research with Sitka spruce has shown a clinal trend of increasing annual height growth with decreasing latitude (Burley 1966b), longer growth period (Lines and Mitchell 1966) and increased frost susceptibility (Wood and Lines 1959). These trends are mainly due to the influence of daylength on the cessation of the growth period.

Temperature was chosen as the variable for investigation, since temperature and moisture supply are thought to be the two main climatic factors which influence the vigour of the species as an exotic, both in Britain and in Europe.

The aim of this study was therefore to define the important formative and qualitative effects of temperature on the growth phases of Sitka spruce. Earlier findings of temperature effects on shoot extension in Sitka spruce (Caldwell 1971) also needed clarification.

The experimental temperature treatments were chosen to represent natural regimes, in an attempt to establish realistic effects of temperature on growth.

This thesis describes three experiments conducted in controlled environment rooms. Clonal material, a full range of provenance seedlings and diallel-cross progeny were used in the study, and the opportunity was taken to compare the performance of the diallel-cross progeny in a controlled environment and in the field. The controlled experiments investigate the effects of temperature on three phases in the life cycle :-

1) flushing and shoot extension
2) growth cessation
3) breaking of dormancy.

The field study together with the collection of climatic data, allows for the comparison of growth between the two environments and the response of different age

plants. The climatic factors influencing extension growth of Sitka spruce in the field can also be elucidated.

Controlled environments are useful tools for separating environmental factors that influence plant growth. In nature radiation, temperature, humidity and other factors are so interrelated that it is impossible to determine the effect of a single factor on plant growth. Only in a controlled environment can one factor be varied while others are held constant.

Results from controlled environment experiments cannot be extrapolated directly to field conditions, but they allow identification of those factors which have the most important effects on a particular process or a particular stage of growth.

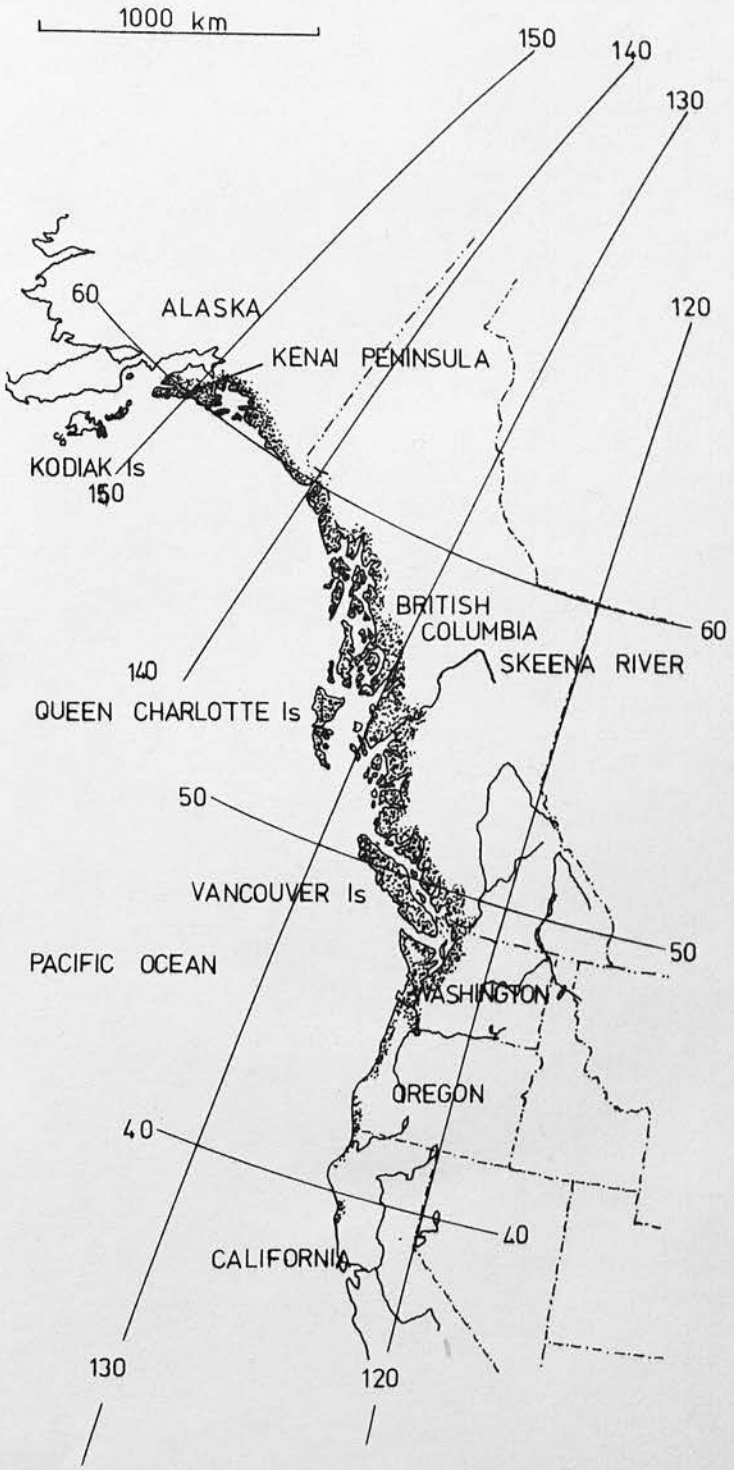
CHAPTER 2. THE SPECIES - SITKA SPRUCE.

2: 1 Natural range.

Sitka spruce, *Picea sitchensis* (Bong.) Carr., the largest of the spruces, is a native of North America and was discovered in the Puget Sound area of Washington in 1792. Halliday & Brown (1943) concluded that Sitka spruce inhabited a southern coastal refuge during the Wisconsin glaciation and that it followed the retreating ice along the coast to Alaska, a process which is still continuing on Kodiak Island in the Aleutians. Daubenmire (1968) however, cites evidence that indicates the survival of *P. sitchensis* through at least the last glacial advance on nunataks, well scattered along the coast from Puget Sound to Juneau, Alaska. Post-Wisconsin peat pollen records show its occurrence in this belt immediately following deglaciation which appears to have happened simultaneously along the coast.

Today, Sitka spruce is found along a narrow coastal belt, from Kodiak Island and the Kenai Peninsula, Alaska (61°N) to Mendocino County, California (39°N)(See Map - Figure 2:1). Although the latitudinal range of the species is long (2,400 km.) it extends inland only a short distance, and is closely associated with the 'fog belt'. The maximum extension inland of 160 - 200 km. occurs in Alaska. Towards the south the range is confined to a belt 50 - 60 km. from the Pacific coast, on sites following coastal streams (Ruth 1958). In addition, the species occurs on the offshore islands of British Columbia, such as Vancouver Island and the Queen Charlotte Islands.

FIGURE 2:1 Range of Sitka spruce



The altitudinal range of Sitka spruce is from sea level to 600 m., still within 8 - 9 km. of the coast, and reflects the specific demand for an equable climate (Schober 1962). At high elevations timber quality and quantity are poor and the upper elevational limits decrease southwards.

Throughout its distribution, Sitka spruce occurs in association with Western Hemlock (Tsuga heterophylla (Raf.) Sarg). In Oregon, Washington and British Columbia Thuja plicata (Donn.), Pseudotsuga menziesii (Mirbel) Franco, Abies grandis ((Dougl.) Lindl.) and A. amabilis ((Dougl.) Forbes) form mixed stands, while in Alaska Chamaecyparis nootkatensis ((D. Don) Spach) and Tsuga mertensiana ((Bong.) Carr.) are important associated species (Schober 1962). On sand dunes and peat bogs along the coast, Sitka spruce competes with Lodgepole pine (Pinus contorta Dougl.).

Day (1957) discusses the status of Sitka spruce in the forest, relative to its associated species. He found that in mature forest, the less shade-tolerant spruce is set as a co-dominant within the matrix of more shade-tolerant trees, of which hemlock is the more abundant in most situations. The greater growth vigour of spruce relative to other species, enables it to assume a dominant position in the canopy, providing the fertility of the site is favourable. Site tolerance and the natural regeneration of the species are described fully by Day (1957) and Schober (1962).

2: 2 Climatic influences.

Schober (1962) provides a detailed account of the climatic

requirements of Sitka spruce and emphasises the connection between its natural distribution and a moist, cloudy and rainy coastal climate, with relatively equable temperatures throughout the year. Annual temperature and rainfall data for the latitudinal range are given, and show that temperature variation is most marked in the winter months, with mean January temperatures of 8.3°C at Eureka, California, compared to -2.9°C at Juneau, Alaska. Temperature dispersion during the growing season however, is less marked, due to the influence of the warm Kuroshio drift*, resulting in maximum dispersion throughout the range in May of 2.9°C, June 2.4°C, July 4.6°C and August 4.9°C.

The length of the growing period (days with mean temperature >10°C) depends closely on latitude, and ranges from 112 days in Alaska to 224 days in California. Ruth (1958) considers that the shorter growing season in the north is partly offset by long summer days. The growth period is substantially shorter than the frost-free period, which varies from 163 to 276 days, from Alaska to California. The large climatic gradient existing along the distribution range of the species and the genetic adaptation of the species to it, markedly influence the choice of provenance for afforestation in the United Kingdom.

The annual rainfall over the range of the species is very high, at 1,700 to 2,400 mm, excepting the southern limit in California, which receives about 1,000 mm. and the Queen Charlotte Islands whose annual rainfall totals 1,400 mm. Notably high rainfalls of 3,100 mm. are recorded at Quinault,

* and the cool Californian current

Washington, at the foot of the Olympic Mountains. The rainfall during the growing season constitutes 40 per cent (800 mm.) of the annual rainfall in Alaska, compared to only nine per cent (91 mm.) in California. The tendency to summer drought in the Sitka belt, is somewhat offset by frequent thick fogs, that extend inland up to 30 km., and which contribute to the high atmospheric humidity of the Pacific coast.

Maximum development of Sitka spruce is found in the Queen Charlotte Islands and on the Olympic Peninsula of Washington. In this area, the climatic conditions are similar to those in parts of North West Europe (Day 1957), and this accounts for the success of the species as an exotic in Britain and Scandinavia.

In conclusion, it can be seen that the range of Sitka spruce is characterised by high atmospheric humidity, relatively high winter temperatures and high precipitation, which suggests a high moisture demand by the species.

2: 3 Intraspecific variation.

There has been little reference in the literature to morphological variation in Sitka spruce and despite the extensive latitudinal range, no geographic varieties have been distinguished (Wright 1955).

The most acceptable concept of variation in forest trees is that climate has a continuous variation pattern and tree growth is related to climate. Although the nature of its range predisposes the species to a clinal type of variation, Burley (1965b) considered that the concepts of

clinal and ecotypic variation are not mutually exclusive. Discontinuous environmental factors may be superimposed on the clinal pattern to produce genetic changes that can be recognised as ecotypes.

Reviews of provenance research have been given by Burley (1965b) and Lines (1964), who refer mainly to studies conducted in Europe. The growth pattern of provenances through the range varies clinally with latitude - correlations have been found between daylength and growth cessation (Burley 1966b, Kraus & Lines 1976, Pollard et al. 1975). In northern sources, Kraus & Lines (1976) found a discontinuous pattern of growth cessation, unrelated to latitude, indicative of the survival of the species on nunataks. Time of flushing is an adaptive response to spring temperature. Southern provenances are more subject to frost damage, both at the beginning and end of the growing season, than provenances from Queen Charlotte Islands and Alaska, when grown in W. Europe, yet still show greater height growth and volume production if they survive (Lines 1964). Provenance differences in leader and branch growth almost certainly reflect inherent adaptive differences in the duration of needle primordia deposition in the winter bud (Burley 1966b, Cannell & Willett 1975).

Vaartaja (1959) demonstrated the existence of photoperiodic ecotypes in Sitka spruce, when comparing the ratio of height growth under long and short days for seedlings of an Alaskan and an Oregon provenance. In a

detailed analysis of bud formation in individual provenances, Burley (1966b) shows that ecotypes may have developed in response to local environmental selection pressures. He also suggests that local clines at one latitude may develop in response to continuously varying factors such as altitude.

Cannell (1974) regarded the eight year old provenances of Sitka spruce that he studied from Oregon, British Columbia and Alaska, to be physiological ecotypes in respect to branch development, distinguished only by their different height growth in given environments. Interactions between factors affecting height growth, as well as inherent differences in lateral branch frequency were thought to lead to intraspecific differences in shoot production and yield.

Variation by natural hybridisation with white spruce (Picea glauca (Moench) Voss) has been reported in Alaska by Little (1953), who named the hybrid Picea x lutzii. In British Columbia, the clinal pattern of variation between coastal Sitka spruce and montane white spruce, in the Nass and Skeena rivers region, is probably the result of introgressive hybridisation (Roche 1969). Introgression between Sitka spruce and Picea engelmannii and P. mariana is also thought to have occurred in this area (Fowells 1965).

2: 4 Sitka spruce in Britain and Europe.

Sitka spruce was introduced into Great Britain in 1831 by David Douglas, and by the end of the nineteenth century was

used in plantations. It is the most important conifer species planted in Britain today, is usually easy to establish and will grow satisfactorily under a wide range of conditions. The earliest large scale plantations of the species were established on relatively fertile slopes in the western half of Britain, where its high moisture requirement is easily satisfied. On good sites Sitka spruce is a high volume-producer and yields up to 25 cubic metres per hectare per annum. Most of the present and future planting by the Forestry Commission is taking place in Scotland. In the season 1973-1974 Sitka spruce accounted for 67 per cent of trees planted in Great Britain, making a total of 275,000 hectares planted with this species. Importation of seed prior to 1923 was from Washington and Oregon, but these provenances were found to be susceptible to frost-damage, and thereafter, apart from small quantities imported from Washington, the hardier but slower-growing Queen Charlotte Islands provenances have been the major source. Alaskan provenances have been planted on more exposed sites in north Scotland, within the last ten years, and the demand for a provenance that is fast-growing, exposure-resistant and frost hardy will increase as planting is extended to more marginal sites (Fletcher & Faulkner 1972).

The general form and vigour of the species can be regarded as good, but this can be improved through selection and breeding. Sitka spruce is the most important conifer in the forest industry and provides valuable 'whitewood' timber both for the sawmilling and pulping industries. The timber

is suitable for general building purposes, but only slow-grown material is suitable for joinery and high-class structural work (Fletcher & Faulkner 1972).

The disadvantages of Sitka spruce as a forestry species include its susceptibility to windthrow on poorly drained soils, due to shallow-rooting on these sites, and also that it is often held in check by Calluna on heath-lands. The species is not seriously affected by pests, although Elatobium abietinum can cause considerable defoliation in years of severe attack.

Sitka spruce is also important in western European forests, giving higher yields than the native Norway spruce (Picea abies (L.) Karst), and is more resistant to wind exposure. In Germany, Schober (1962) concluded that north Washington and Queen Charlotte Islands provenances were the most suitable for general planting. In Norway and Sweden, Alaskan provenances can generally survive the lower winter temperatures, in contrast to more southern sources.

2: 5 Seasonal growth cycle.

The seasonal pattern of shoot growth of Sitka spruce is characterised by a spring flush of the winter buds, followed by a period of determinate shoot elongation, which is completed relatively early in the frost-free season. Occasionally late-season shoot growth occurs, resulting from the flushing of current year buds in response to favourable environmental conditions. Such shoots are often killed by autumn frosts, as they have insufficient time to harden. A period of dormancy follows bud formation,

during which the chilling requirement for bud-break and normal shoot growth must be satisfied.

Considering the wide-scale use of Sitka spruce as a productive forest species, apart from the comprehensive research by Burley (1966a, 1966b), it is only relatively recently that studies of the seasonal growth cycle have been made (Cannell & Willett 1975, Pollard et al.1975, Owens & Molder 1976).

The initial starting capital for the first season of growth is the embryo and female gametophyte tissue. The patterns of variation in seed and embryo characteristics have been reported by Burley (1965a). An important differentiating factor in the growth of young seedlings of Picea species, is the ability for 'free' growth, as described by Jablanczy (1971). Free growth involves the initiation and development of new needles without interruption, on a continuously expanding stem, and in the first year is the only mode of growth from germination to budset.

For subsequent seasons the terminal bud is the starting capital, because it contains the telescoped shoot that will expand during the following season and the needle primordia that will develop into functional needles. Free growth may augment the flush of predetermined new growth in young seedlings, and has been reported in Picea glauca up to five years old (Neinstaedt 1966).

The rate of free growth in Sitka spruce was found to be fairly consistent amongst a set of provenances in a controlled environment, during the first 12 weeks of growth

(Pollard et al.1975), though no provision for the effects of variation in temperature or photoperiod was made. Response to an artificially declining photoperiod showed a four hour difference in critical daylength between northern and southern provenances. Two year seedlings grown under natural conditions however, exhibited differences in rates of growth as well as a clinal relationship with latitude for date of growth cessation (Lines & Mitchell 1966, Kraus & Lines 1976), indicating a photoperiodic mechanism in the cessation of free growth, with a consequent difference in height growth through the range.

Development of the shoot apex in seedlings of Sitka spruce in New Haven, Connecticut, is described in detail by Burley (1966a). Anatomical evidence confirms morphological evidence for a pattern of developmental variation that is closely related to the natural distribution of the species. The three stages of seasonal periodicity in conifer shoots reported by Parke (1959) for Abies concolor were found to be applicable to Sitka spruce, namely 1) rest 2) elongation and bud scale formation and 3) production of cataphylls and telescoped shoot. Elongation and needle extension continued into July for seedlings from Alaska, and into September for those from California. Variation in the time of bud formation was closely correlated with the latitude of seed origin, extending over a period of three months for seedlings from 47 provenances; this correlation indicates strong photoperiodic control. Southern provenances continued to form needle primordia until December whereas

northern provenances stopped in October. The rest stage extended until April, with only two weeks separating the provenances in time of flushing. The geographic pattern of flushing was related to the native temperature regime. In some southern provenances a small number of leaf primordia were initiated during the first flush of spring growth.

A study of needle initiation in buds of eight year old Sitka spruce of five provenances, revealed similar findings to those of Burley (Cannell & Willett 1975). The sequence of events was as follows: by early May the apical domes were enlarging and producing scale primordia. Formation of scale primordia continued throughout May and most of June, and on June 25 the first needle primordia were initiated. Ten per cent of the needle primordia were present by mid-July. Needle formation slowed during September and by mid-October all buds were in the winter state. Differences in the timing of this sequence of events between provenances were found, but the rates of needle primordia formation were similar. Fourteen days separated Alaskan provenances from British Columbia and Oregon at the start of needle primordia formation, and 14 - 28 days at bud formation. With decreasing latitude there was a tendency for the number of protective scale primordia to decrease and the number of needles per bud to increase - twelve days difference in duration through the range resulted in 70 more needles being formed by an Oregon provenance than one from Alaska. Differences in the final

length of branches which had extended from buds formed the previous year, were very closely related to differences in numbers of predetermined needles.

The phenology and histological development of buds in mature Sitka spruce in British Columbia, has been described by Owens & Molder (1976). The phases of development occurred over a longer time period than was reported for eight year old trees (Cannell & Willett 1975). The time from the first cell divisions within the bud to the cessation of leaf primordia initiation, spanned approximately 33 weeks, from late March to mid-November. The onset of growth in the spring, as determined by mitoses within the bud, is shown to occur some weeks before noticeable bud swelling or flushing. It may be that the time of flushing is affected by variations in the time when mitosis starts, and or the rate of subsequent shoot development within the bud.

Thus the development of the bud in Sitka spruce follows a continuous, well-defined pattern, with the same sequence of events occurring in all seed sources. It is the difference in the timing of these events between seed sources that causes variation in the duration of growth. The dates of flushing and bud formation determine the susceptibility of the species to spring and autumn frosts, respectively.

Burley (1966b) examined the relationship between bud components and bud size, and in turn, bud size and height growth. He concluded that the number of bud scales and

primordia contribute significantly to bud diameter, but there was no significant difference in bud diameter between seed sources. Large seedlings were found to develop larger buds, at least for the first two seasons, and this characteristic presumably increases the height differential in subsequent seasons.

Cannell (1974) showed that the varying height growth, crown form and total needle and wood volumes in different provenances of eight year old Sitka spruce were related to the number of predetermined needle primordia. Shoot length differences were determined more by differences in numbers of stem units than by the extent to which these elongated. The number of lateral branches was a function of the length of the parent shoots from which they grew. Hence provenances with large numbers of needles in their leader buds produced long leaders, with relatively large numbers of long branches, which bore relatively large numbers of sublaterals.

Under controlled environmental conditions, Burley (1966b) found little variation in absolute rates of height growth between provenance seedlings. Total height growth increased clinally north to south, and these results parallel those of Aldhous (1962), Schober (1962), Lines & Mitchell (1966) and Kraus & Lines (1976).

The foregoing research demonstrates that the major factor affecting the total height growth is the duration of needle primordia deposition in the winter bud, together with the ability of young seedlings to make free growth, and the ability of southern provenances to produce lammas flushes.

Early work by Hiley & Cunliffe (1923) describes the seasonal height growth of young Sitka spruce in the Oxford area. Maximum extension growth occurred during the latter half of June, with 80 per cent of the total growth made by mid-July. Rates of growth were most closely correlated with maximum shade temperature. A similar study (Godman & Gregory 1955) in S.E. Alaska showed a leader-growth period of 10-12 weeks, with lateral shoots ceasing slightly earlier.

The pattern of seasonal girth growth in Sitka spruce has received little attention. In Alaska the grand period of radial growth began before flushing of the leader and continued beyond the time of bud formation. The rate of growth was fastest during the latter part of the period (Godman & Gregory 1955). In a study of height and radial increment in 30 year old Sitka spruce, Fraser (1970) found most radial increment in periods of rainfall and high atmospheric humidity.

Although the duration of the active period of shoot growth may be photoperiodically controlled, the amount of height growth made may be modified by environmental conditions prevailing during the growing season and by other site factors.

CHAPTER 3. THE EFFECTS OF TEMPERATURE ON FLUSHING AND EXTENSION GROWTH OF SITKA SPRUCE IN A CONTROLLED ENVIRONMENT.

3: 1 Literature review.

As briefly mentioned in Chapter 2: 5 the main determinants of height growth in most coniferous species are 1) the initial starting capital of potential growth material, which is related to the temperature and photoperiodic conditions during bud induction and maturation, 2) the rate of growth, 3) the duration of growth, and 4) the conditions prevailing during the growing season. The duration of growth, which has been shown to be the most important factor controlling extension growth in Sitka spruce (Burley 1966b) is determined by the developmental behaviour of the terminal bud.

Numerous reports acknowledge that the period of active growth in Sitka spruce occurs during a short part of the frost-free period and terminates while temperature conditions are still favourable for growth (Lines & Mitchell 1966).

The physiological cycle of a species is the outcome of adaptation to a climatic cycle in the natural habitat. Because it is rate limiting to most metabolic processes, temperature must play an important role in the rate of growth. Fluctuations in air and soil temperatures influence the growth of trees by altering the rate of photosynthesis, respiration, cell division and elongation, enzymatic activity, chlorophyll synthesis and transpiration. Growth usually increases with an increase in temperature,

until an optimal temperature is reached, and then declines rapidly.

Temperature and bud morphogenesis.

The morphogenetic phase of bud development is probably the most important factor controlling shoot growth in northern conifers (van den Berg & Lanner 1971). Shoot extension growth in Picea species in year n + 1 has been shown to be greatly dependent on temperature conditions during year n, especially at the time of bud differentiation and bud maturation (Dormling et al. 1968, Skre 1972, Heide 1974b, Pollard & Logan 1977).

The effects of temperature during this period are not documented for Sitka spruce, though its importance as an influence is acknowledged (Pollard et al. 1975). In white spruce (P. glauca (Moench) Voss) and black spruce (P. mariana (Mill.) B.S.P.) the optimum temperature for needle initiation is 25°C or above, with slower rates at temperatures of 10°-20°C (Pollard & Logan 1977). Temperature did not appear to affect the duration of initiation in these species. The optimum temperature during bud differentiation (up to 24°C) in Norway spruce was increased with a decrease in time, indicating a heat sum effect (Heide 1974b). Delayed flushing in plants with buds matured at high temperatures suggests they had entered a deeper state of dormancy than those matured at low temperatures, a similar result to that of Dormling et al. (1968).

It should be noted here that there is a close

interaction between temperature and photoperiod during bud maturation and prior to flushing, a fact that can lead to diverse environmental requirements when studying the growth of plants (provenances) under experimental conditions. For example, in Norway spruce a combination of short photoperiods and high temperatures in year n, resulted in early flushing and the greatest shoot growth in the first flush of second-year seedlings, and had similar effects on the second flush (lammas shoots) (Heide 1974b). Photoperiod during the current growing season can modify the influence of previous temperature/photoperiod conditions, hence flushing in short days reduces the amount of extension growth in Norway spruce (Dormling et al. 1968). However, the effect of temperature and photoperiod conditions in year n has been shown to affect growth in years n + 2 and n + 3, though increasingly in an indirect manner (Heide 1974b).

Temperature and flushing.

Although several publications refer to genotypic variation in flushing of Sitka spruce (Aldhous 1962, Burley 1966a, Lines & Mitchell 1966, Schober 1962) little is known of the effect of varying temperature regimes on bud burst.

Lines & Mitchell (1966) ascribe the earlier flushing of Sitka spruce in the field in 1961 compared to 1960, to the warm early spring in the former year. Burley (1966b) working with Sitka spruce seedlings in the open, concluded that the time of flushing is an adaptive response to spring temperatures in the native habitat. Similar conclusions are drawn by Cannell & Willett (1975), who

suggest that northerly ecotypes require a smaller heat sum to begin growth each season, thus explaining the earlier flushing of northern provenances as compared to those from Oregon.

The effect of artificial treatments on the flushing response of Sitka spruce has also been examined by Burley (1966b). Two relatively similar temperature conditions were used; a controlled environment room with a day/night temperature regime of 27/15°C, and a greenhouse where day temperature ranged between 20°-25°C and night temperature was maintained at approximately 15°C. Conditions in the controlled environment room promoted earlier flushing than in the greenhouse, but rate of flushing showed little variation between treatments.

Temperature control in the life cycle of Norway spruce (Picea abies (L.) Karst) has been studied in greater detail than for Sitka spruce. Zumer (1968) made a comprehensive study of the effect of a range of constant temperatures from 12°- 24°C, on the period of flushing and the distribution of bud break, within four year plants of Norway spruce. The pattern of bud break from the base of the plant to the terminal was not affected by temperature, but higher temperatures were found to decrease the period of flushing, and the time lapse between lateral and terminal bud break.

Many reports on the growth of Sitka spruce and related species under artificial conditions, describe the rate and duration of height growth, but make no reference to the

timing of bud break. Extensive work by Dormling et al. (1968) on Norway spruce in Sweden, demonstrates how the annual vegetative cycle can be compressed into a period of 15 weeks. No precise experiments on the temperature control of flushing have been made, but the decisive influence of both temperature and photoperiodic conditions during bud maturation, on the time of initiation of flushing is emphasised. Similar results were found by Burley (1966b) for Sitka spruce, and Simak (1970) for Larix decidua (Mill.).

The interdependence of environmental effects on the rate of flushing in Douglas fir has been proved by Campbell & Sugano (1975). Chilling, photoperiod and flushing temperature all played a part in the rate of bud flushing. At all flushing temperatures the effect of chilling and lengthened photoperiod was to increase the rate of bud burst.

Temperature and height growth.

Observations on the shoot extension of trees may take several forms. The study of seasonal growth periodicity associated with the rate of growth, describes the cumulative growth of a species over time. The study of diurnal periodicity in growth allows the relationship between specific day/night temperatures and shoot elongation to be elucidated.

With the aid of controlled environments the effects of temperature on height growth can be investigated from four aspects, namely, day temperature, night temperature, thermoperiodism or the day/night temperature relationship,

and accumulated energy input.

Brix (1972) showed that for Sitka spruce seedlings from Terrace, British Columbia and from Queen Charlotte Islands, the optimal temperature for height growth was 18°-24°C. Higher temperatures resulted in reduced height growth and a marked decrease in dry matter production. In an experiment with four coniferous species, including a number of Sitka spruce provenances, Mergen et al.(1974) obtained greatest height growth at 20°C constant. They suggested that Sitka spruce is less dependent on a day/night differential than white spruce and Jack pine and that the height growth made reflects total heat sum. However, as the relative humidity was set at 50 per cent, a proportion of seedlings died, particularly in the 30°C treatment, which indicates that the plants may have been more affected by moisture stress than temperature.

The optimal temperature for growth of Norway spruce has been shown to be constant 20°C (Dormling et al.1968), while Heide (1974a) studying the same species, found the optimal temperature for apical growth to be 21°C in all ecotypes, but with little difference over the range 18°-24°C. These contradictory results within species are probably due to differing values of other environmental variables, such as daylength and vapour pressure deficit.

Night temperature has been shown to be important in controlling the growth of Engelmann spruce (Picea engelmannii Parry) (Hellmers et al.1970). A day/night regime of 19°/23°C resulted in greatest growth, suggesting

that night temperature may be the factor that influences the growth of spruce in the field. Such a temperature inversion however is unnatural and the validity of extrapolation of such results to the field is questionable.

Numerous studies have shown that the relationship between day and night temperatures, influences shoot growth of trees. Brix (1972) demonstrated the beneficial effect of a day/night temperature differential in Sitka spruce seedlings, both for height growth and dry matter production. A 24°C day and 18°C night proved optimal, and a cool night temperature of 13°C relieved the deleterious effects of a 28°C day. These findings differ from those of Mergen et al. (1974).

The accumulated effect of temperature on growth can be estimated by totalling the degree-hours, over some threshold value. Armson (1962) discusses the advantages of using such a temperature index, rather than the conventional method of relating temperature to growth per day. He demonstrates a closer correlation between dry weight increment and heat sum for white spruce seedlings (Picea glauca (Moench) Voss), than between dry weight increment and calendar days.

The usefulness of heat sum as an expression of the relationship between temperature and plant growth is questioned by some research workers. Went (1953) considered the heat sum method to be invalid as it ignores the differentiation between day and night temperatures and that optimal day - night temperatures are strongly dependent

upon the light intensity i.e. at lower light intensities optimal temperature may be decreased. This may be true for some species but with a doubling of light intensity from 450 ft. - c. to 1000 ft. - c., Sitka spruce seedlings varied little in height growth, and optimal temperatures remained the same (Brix 1972).

It is generally considered that more shoot elongation occurs at night than during the day. Provisional results of shoot growth in 13 year-old Sitka spruce, using an automatic measuring system (Milne et al. 1977), show maximum growth rates in late evening, although recorded shoot lengths are not significantly different during day and night. During two consecutive days measurements, leader growth totalled 8.2mm, with peaks in the growth rate between 2100 and 2300 h., followed by a decline and shrinkage until approximately noon. Mork (1941) observed a distinct daily rhythm in shoot elongation of Norway spruce, with maximal growth occurring at night.

When considering the effect of temperature on the growth of trees, the modifying effect of air temperature on soil temperature must not be overlooked. For Sitka spruce a soil temperature of 16°C provides a satisfactory environment for raising seedlings (Herbert 1971). Coutts & Bowen (1973) report rapid increase in root growth of Sitka spruce seedlings as soil temperatures increase from 6°- 18°C, with little further effect at higher temperatures. Soil temperatures were shown to have a significant effect on total growth of white spruce seedlings (Chalupa & Fraser

1968). With constant air temperature of 21°C, the greatest height growth and dry matter production occurred with the lowest soil temperatures of those tested, i.e. 10°C and 18°C. With an increase in soil temperature, the percentage of dry matter in the shoot decreased.

Several physiological explanations for the varying growth responses of tree species to temperature have been put forward. Kramer (1957) did not consider the increased use of assimilates in respiration at high night temperatures, to be the only factor responsible for reduction in growth of loblolly pine. He saw the need for accurate photosynthesis/respiration measurements.

The elongation of apical shoots in Norway spruce, has been divided into three growth phases by Mork (1941). The first and last phases increase and decrease respectively as a function of time, and the main phase comprising 60 per cent of the total annual growth occurs between these two phases, when growth is constant as a function of time. During this main period of growth, daily shoot elongation was highly correlated with the mean temperature of the six warmest hours of the day. Dahl & Mork (1959) discuss the physiological mechanism responsible for this correlation during the main growth phase. The hypothesis is advanced that energy supply by respiration constitutes the limiting factor of growth. The respiration of Norway spruce was determined at six temperatures, and the daily amount of respiration as a function of temperature was found. A linear relationship between daily

growth and respiration supported the hypothesis.

Thus it can be seen that temperature plays an important role during the active period of extension growth of trees. Several workers have studied the effect of substituting periods of high or low temperature during the active growth period, and this approach is discussed later as it relates to growth cessation.

3: 2 Introduction.

An earlier experiment carried out by Caldwell (pers. comm. 1971) studied the effect of temperature on the growth of Sitka spruce grafts. Three temperature treatments were used - constant 20°C, constant 8°C, and 20°C day/8°C night. Results indicated that high temperatures decrease the time required under otherwise favourable conditions for flushing to occur. Warm temperatures were found to induce flushing from the base of the plant upwards, whereas plants under constant 8°C flushed in the same manner as control plants out of doors, that is from the terminal downwards.

The effect of these temperatures on height growth resulted unexpectedly in greater extension and a longer growth period at constant 8°C than under constant 20°C. This response may in part have been caused by the varying humidity conditions in the growth rooms - a constant 80 per cent relative humidity at all temperatures, resulted in a vapour pressure deficit (VPD) of 4.7mb at 20°C and 2.2mb at 8°C. If the VPD is not constant with varying temperatures or has a high value (>5mb), growth results may be in response to VPD rather than the temperature

conditions, through its effect on stomatal conductance and consequently photosynthesis (Neilson & Jarvis 1975).

The inadequacies in these experimental conditions and the limited plant material studied, made a further experiment using transplant and clonal material desirable. This first experiment was designed to investigate the effect of temperature on the initiation of growth, the rate of growth and the duration of growth of Sitka spruce in a controlled environment.

3: 3 Materials and Methods.

Treatments

Three temperature treatments (Table 3: 1) were obtained using two growth rooms, one set at constant 20°C, the other at constant 8°C. The plants subjected to a variable day/night temperature regime were transferred to and from the relevant growth rooms daily.

Table 3: 1 Experimental treatments in controlled environment rooms.

	i	ii	iii
Day temperature (°C)	20	8	20
Night temperature (°C)	20	8	8
Relative humidity (%)	91	81	91/81
Vapour pressure deficit (mb).	2.0	2.0	2.0
Light intensity - fluorescent (warm white)	18,000.	18,000.	18,000.
(lux) - day (tungsten)	100.	100.	100.
Air flow ($m\ s^{-1}$)	0.1	0.1	0.1

All temperature treatments received a 17h photoperiod

as follows:-

2.5h	daylight, tungsten filament bulbs
12h	fluorescent tubes and tungsten filament bulbs
2.5h	tungsten filament bulbs
7h	darkness.

The tungsten filament bulbs provided a far red supplement. The growth rooms were balanced for light intensity and air flow - see Appendix 3 for details.

Plant material.

Post-dormant clonal cuttings and diallel-cross progeny of Sitka spruce, with pre-histories as listed in Table 3:2, were potted in 7" diameter pots in December 1972 - January 1973, using a 50:50 coarse sand and peat mixture. Blood and bone fertiliser was added (1 kg m^{-3}) to the compost, together with a nutrient mix, the final pH being 5.5. The soil was maintained at field capacity by daily watering, and additions of liquid fertiliser were made twice weekly.

The plants - six plants of each clone, and five of each of the five progenies: AD, AG, HG, KH and CK - were allocated randomly to treatments and re-randomised within treatments weekly.

Measurements.

1) Initial measurements of height, and stem diameter at the mid-point of the 1972 leader, were made on all plants.

2) The progress of flushing was recorded daily as one of five stages (adapted from Lines & Mitchell 1966):-

i) Winter state i.e. bud showing no signs of

Table 3:2 Details of plant material.

S.S. Clone 8000 -	1 year cuttings, in greenhouse until Sept. 1972, then "plunged" out of doors. Buds showing signs of lammas growth. Approximate height 21 cm. Provenance - Queen Charlotte Islands, British Columbia. Age 8yrs. from seed.
S.S. Clone 8014 -	2 year cuttings, in greenhouse until Sept. 1972, then "plunged" out of doors. Lateral buds of some plants showing lammas growth. Approx. height 45 cm. Provenance - QCI, B.C. Age 6yrs. from seed.
S.S. Diallel - cross progeny -	Five crosses chosen to represent a range of phenotype variation :- AD, AG, HG, KH, CK. 2 year seedlings lifted in Nov. 1972 (Fleet, S.W. Scotland), then placed in cold store at 2°C. Approx. height 30 cm. For a detailed description of the progeny see Samuel et al.(1972).

flushing.

ii) Bud swollen, but not yet burst.

iii) Bud scales reflexed - needles not yet visible, or green colouration showing through thin bud scales.

iv) Needles visible through top or side of bud.

v) Needles clearly visible - bud fully flushed.

Each plant was divided into five sections: the terminal bud, plus four equal sections from tip to base, in order to assess the sequence of flushing through the plant.

The variates in the analysis of variance for flushing were as follows :-

50% T Time until 50% of terminals flushed.

Terfin Mean time until terminal buds flushed.

Terdur Duration of terminal bud flushing.

Totfin Mean time until plant completely flushed.

Totdur Duration of complete plant flushing.

Seqfin Sequence of flushing i.e. totfin minus terfin.

3) When 50% of the plants in any group were fully flushed, weekly measurements of shoot extension began. The experiment was carried out between 24th January and 7th June, 1973, a period of 19 weeks.

4) At the end of the experiment various morphological parameters were recorded (Table 3:3).

Table 3:3. Morphological parameters measured at the end of the experiment.

Stem diameter	-	at point of initial measurement.
	-	midpoint of 1973 leader.
Needle length	-	mean of 10 needles per plant, from middle of current season branch.
Branches	-	length of current season branch.
	-	length of 1973 shoot, with 1972 origin.
Buds	-	number of subterminals and internodal buds on leader.

	-	number of lateral buds on 1973 shoot
	-	number of lateral buds on a 1973 shoot with 1972 origin.
Dry weight	-	100 needles from middle of current season branch.
	-	total weight of current season branch.
Growth points	-	number per plant.

After a short period in a cool greenhouse, the plants were placed out of doors.

Analysis.

The data collected were subjected to analysis of variance. The relative height growth rates (RHGR) of all plants were determined from the relation:

$$RHGR = \frac{\log_e H_2 - \log_e H_1}{T_2 - T_1} \quad (cm \cdot cm^{-1} \cdot yr^{-1})$$

where H_1 and H_2 refer to the heights at the beginning and end of the experiment, and the time interval = 1, representing a single growing season. This time interval was chosen to allow a direct comparison to the growth of similar plants in the field (Chapter 4).

In order to compare the varying responses of the different plant types to the treatments applied, it is necessary to fit an equation to the growth curves observed in the experiment. One such equation which has been shown to be applicable to the growth curve of organisms, is the Gompertz equation (Ricklefs 1967).

This equation is :

$$Y = A + C^* \text{ Exp } (-\text{Exp } (-B(X-M))) \quad \text{Gompertz}$$

in which A = the lower asymptote

C* = the total height gain

B = the slope

M = associated with length of growth period.

These parameters of the curves may then be used to analyse the differences between the curves.

Some mortalities occurred in the Sitka spruce progenies during the experiment. Four plants (3 x HG, 1 x KH) failed to flush and a further six plants (2 x CK, 3 x HG, 1 x KH) were subsequently lost. These missing values did not seriously affect statistical analysis, apart from the reduction in plants of HG at 8°C from five to one.

3: 4 Results.

Flushing.

The general stages of growth of the plants under the three temperature regimes are shown in Figure 3: 1.

The length of time in days for the various stages of flushing is shown in Table 3: 4a. Flushing in Sitka spruce was significantly ($p \leqslant 0.01$) retarded in the 8°C treatment compared to either warmer treatment. Although the 20°C treatment appears optimal for flushing it is not separable from the 20/8°C regime (Table 3: 4b).

Differences were detected in the flushing of the Sitka spruce clones; 8014 the older clone reached terminal bud break before clone 8000, but was later to attain full flushing. This was owing to an opposing sequence in the two clones - 8014 buds flushing downwards and 8000 upwards through the plant.

FIGURE 3 : 1 Stages in development of Sitka spruce under three temperature regimes (mean of all plant types).

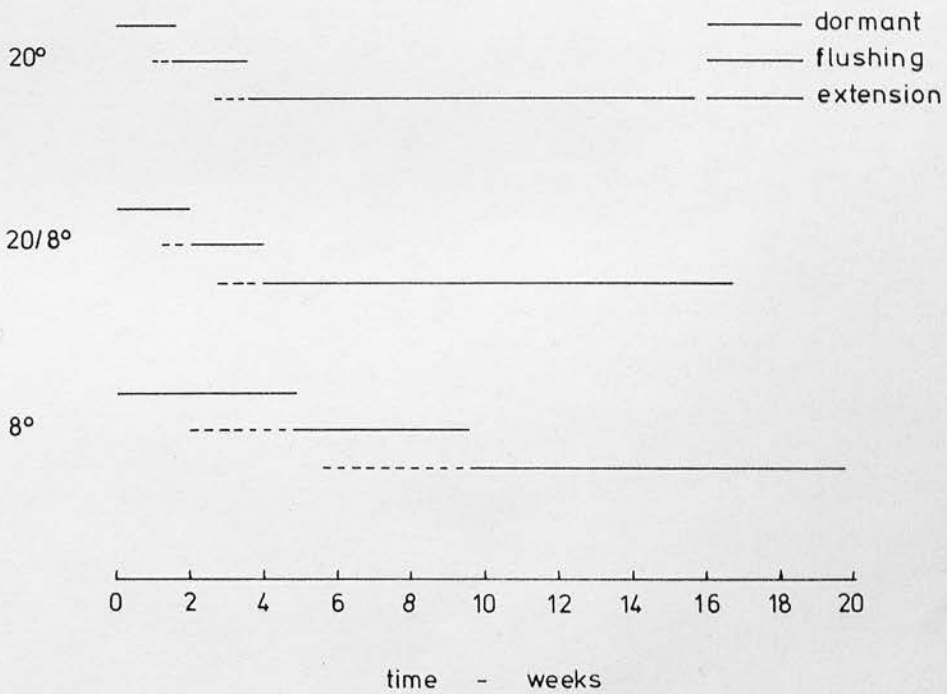


TABLE 3:4a Length of time (days) for stages of flushing.
(No missing values substituted).

			8000	8014	AD	AG	HG	KH	CK
i)	START	20	9.0	8.0	10.4	9.8	10.0	11.0	11.4
		20/8	9.0	8.3	10.6	11.6	10.8	11.8	11.2
		8	15.3	14.3	31.2	32.0	30.4	32.0	34.0
ii)	50% T	20	15.0	14.0	18.0	19.0	13.0	22.0	24.0
		20/8	18.0	17.0	21.0	25.0	20.0	25.0	26.0
		8	45.0	36.0	56.0	67.0	-	60.0	58.0
iii)	TERFIN	20	17.2	15.2	18.4	22.4	14.3	21.6	22.8
		20/8	18.8	18.2	21.0	25.0	20.2	27.0	26.0
		8	46.0	37.7	57.0	67.4	57.8	61.5	59.5
iv)	TERDUR	20	8.2	7.2	8.0	12.6	6.0	10.6	11.4
		20/8	9.8	9.8	10.7	13.4	9.4	15.2	14.8
		8	30.7	23.3	26.7	35.4	29.4	28.8	28.5
v)	TOTFIN	20	17.2	21.2	20.8	24.2	14.7	23.2	25.5
		20/8	19.3	22.7	23.0	26.8	22.8	28.0	30.4
		8	47.8	48.2	62.8	67.4	57.9	66.3	59.5
vi)	TOTDUR	20	8.2	13.2	10.4	14.4	6.3	12.2	14.1
		20/8	10.3	14.4	12.4	15.2	12.0	16.2	19.2
		8	32.5	33.9	31.6	35.4	29.5	32.3	28.5
vii)	SEQFIN	20	0 ↑	6.0↓	2.4↓	1.8↕	0.4↑	1.6↓	2.7↓
		20/8	0.5↑	4.5↓	0.7↑	1.8↕	2.6↓	1.0↑	4.4↓
		8	1.8↑	11.5↓	0.7↑	0 ↑	0.1↑	0 ↑	0 ↑

TABLE 3:4b Levels of significance for stages of flushing. ** $p \leqslant 0.01$, * $p \leqslant 0.05$ (Tukey's test).

	CLONES	TEMPERATURE	PROGENY	TEMPERATURE
i)	* *	20 20/8 8 **	ns	20 20/8 8 **
ii)		NOT	ANALYSED	
iii)	* *	20 20/8 8 **	AG KH CK AD HG **	20 20/8 8 **
iv)	*	20 20/8 8 **	AG KH CK AD HG **	20 20/8 8 **
v)	*	20 20/8 8 **	AG KH CK AD HG **	20 20/8 8 **
vi)	* *	20 20/8 8 **	*	20 20/8 8 **
vii)	* *	20 20/8 8 **	ns	*

Levels of significance between clones and between progeny are shown in Table 3: 4b (full analysis of variance data in Appendix 3). Progenies not shown underscored by the same line are significantly different (Tukey's test, Snedecor 1966). Little or no plant/temperature interaction was found.

Considerable variation in the speed of flushing is seen between the progenies. Progeny HG shows the fastest rate of flushing with AG at the other extreme. The mean flushing duration results of the progeny are similar to those of the clones at 20°C and at 20/8°C. It is interesting to note however that at 8°C, the much retarded start of the progenies resulted in considerably longer terfin and totfin values (Table 3: 4a). No clear pattern for the sequence of flushing can be seen in the progenies. At 8°C all crosses showed an upward sequence through the plant, but response at the warmer temperatures varied.

A difference between the clones and progeny in the mode of flushing at 20°C and 20/8°C was seen, as follows:- (numbers relate to flushing stages as in Methods).

Sitka spruce clones :

ii) bud swells, scales pale brown in colour

iii) scales become thin around sides of bud and green colouration of needles can be seen through scales

iv) scales perforated by needles on side of bud (see Frontispiece)

iv) scale cap pushed upwards with extending needles and detached from base of bud

v) scale cap fallen, needles free

Sitka spruce progeny : buds generally smaller than clone buds

ii) bud swells (Plate 3: 1)

iii) scales reflex from tip of bud outwards

iv) small gap visible in scales at top of bud and green colouration showing through gap (Plate 3: 2)

v) scales fully reflexed, needles spread out widthways and scales remain attached at base of bud (Plate 3: 3).

Differences in flushing between plant types are seen in relation to total temperature sum (Appendix 3). Both Sitka spruce clones began flushing first at 8°C after a relatively small energy input, and completed flushing (totfin) soonest under the 8°C regime. Total duration of flushing however varies, with clone 8000 responding to a lower heat sum than clone 8014 (Figure 3: 2). The progenies all start flushing soonest at 8°C*, but show considerable variation in the degree hours required to complete flushing, both within and between treatments. Progeny CK exhibits the fastest response at 8°C of all plants (Figure 3: 2).

Extension growth.

The effects of the 8°C treatment on flushing were reflected in other aspects of extension growth. All the aspects of extension at 8°C differed ($p \leqslant 0.05$) from the other treatments, except for clone 8014, where differences

* with regard to heat sum

3:1

3:2

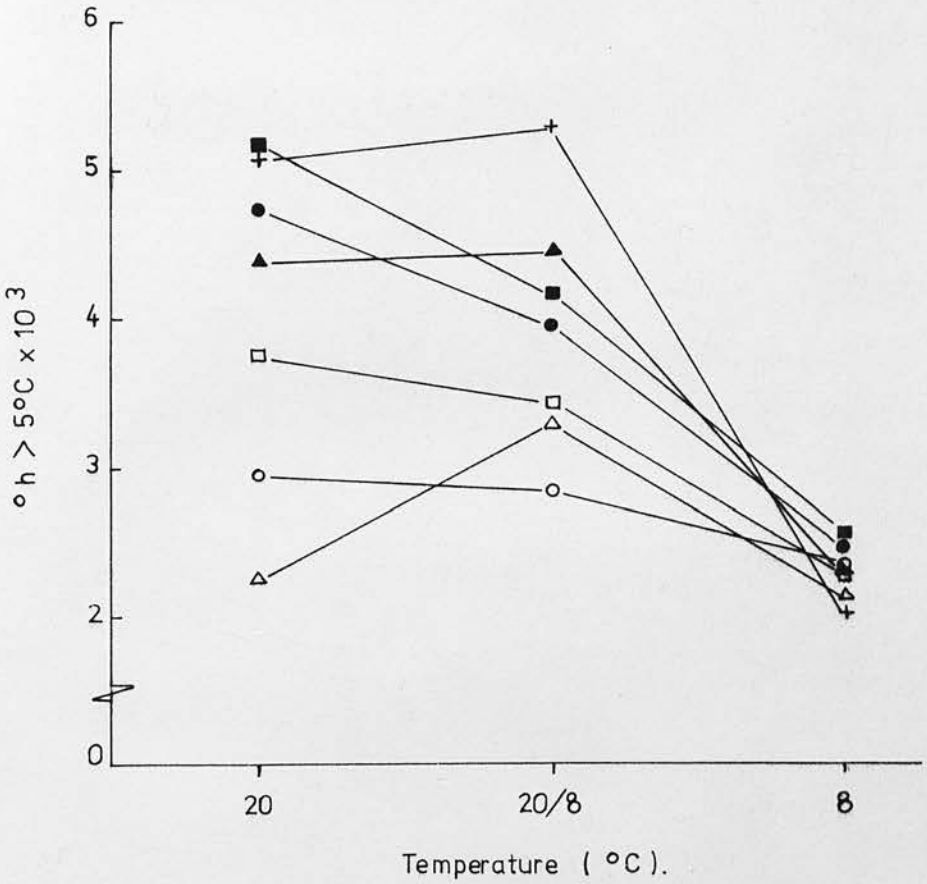
3:3

Plate 3:1 Second stage of flushing - bud swollen.

Plate 3:2 Fourth stage of flushing - needles visible through gap in scales at top of bud.

Plate 3:3 Final stage of flushing - needles extending, remaining bud scales attached at base of bud.

FIGURE 3:2 Degree hours for total duration of Sitka spruce flushing at three temperature regimes.



o clone 8000
● clone 8014
□ AD
■ AG
△ HG
▲ KH
+ CK

occurred only with the 20/8°C treatment (Table 3: 5b).

Highly significant differences in extension growth were found between the clones (Table 3: 5, Figure 3: 3, Plates 3: 4 - 3: 7). Clone 8000 showed maximum growth of all plant types. Clone 8014 exhibited an unexpected response with its longest growth period and greatest height gain at 8°C.

Great variation is seen between the progenies in the start of growth, but despite the variation in the duration of growth, differences in the total height gain within treatments were not large. In all progenies the duration of growth at 20/8°C exceeded or equalled that at 20°C, and in all but AG greater height growth was finally achieved at 20/8°C. From inspection of the growth curves of the progeny (Figure 3: 4), differences in the rate of growth between the cold and the warmer treatments are obvious. At the two warmer temperatures very little difference is seen in either the rate of growth or the amount of height growth made. For comparisons of height growth at 20°C and 8°C, see Plates 3: 8 - 3: 11.

A measure of the growth rate is obtained in parameter B, from the fitting of the Gompertz equation to the growth curves (Table 3: 6). It can be seen that progeny CK at 20°C and at 20/8°C has a considerably higher value of B than any other progeny, expressing its rapid growth over a relatively short period. Differences between other progenies are less and it is interesting to note that progenies KH and HG have their

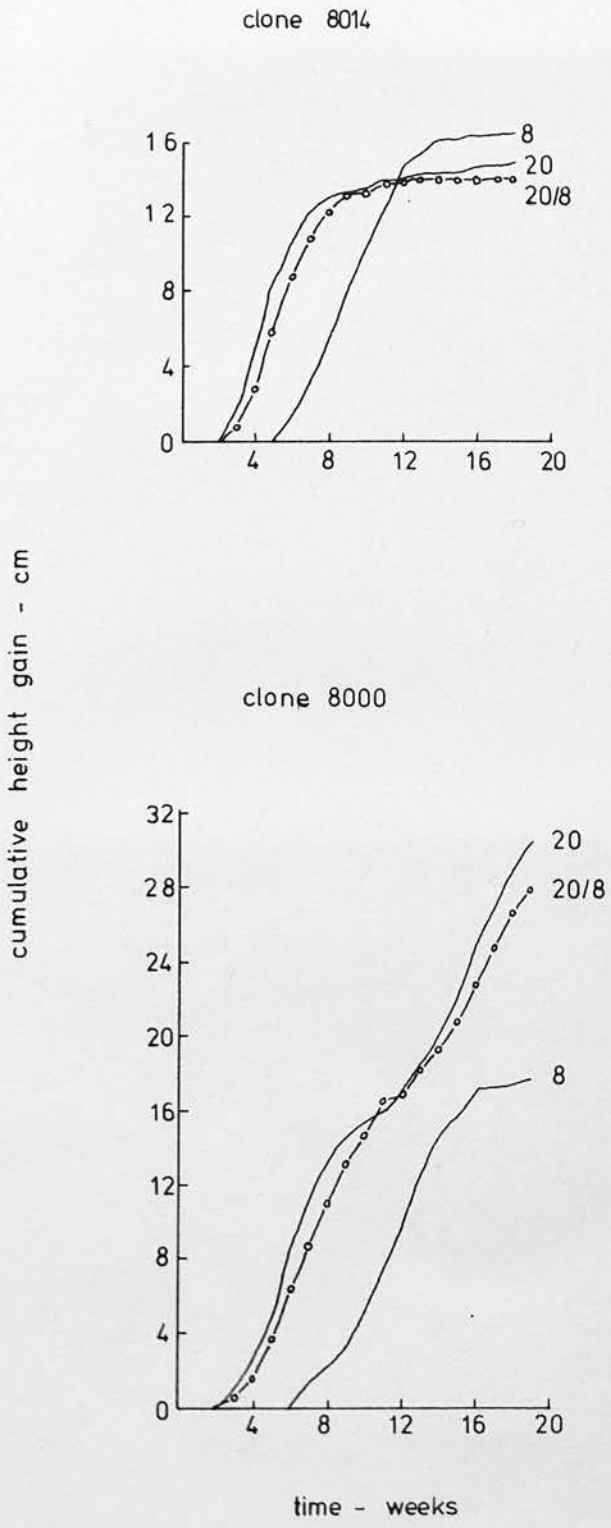
TABLE 3: 5a Growth stages and total height gain - from analysis of variance tables with missing values substituted.

			8000	8014	AD	AG	HG	KH	CK
i)	START	20	2.3	2.0	2.0	3.0	2.0	3.2	3.0
	GROWTH	20/8	2.5	2.0	3.0	3.2	3.0	3.0	3.0
	(WEEKS)	8	6.0	5.0	9.0	9.2	8.0	9.0	8.0
ii)	END	20	18.0	11.2	11.6	12.6	14.0	14.6	9.3
	GROWTH	20/8	18.0	9.0	17.3	14.8	15.0	16.3	10.4
	(WEEKS)	8	17.3	15.0	17.8	17.6	18.0	18.0	18.0
iii)	DURATION	20	15.6	9.2	9.6	9.6	12.0	11.4	6.3
	GROWTH	20/8	15.4	7.0	14.3	11.6	12.0	13.3	7.4
	(WEEKS)	8	11.3	10.0	8.8	8.4	10.0	9.0	10.0
iv)	HEIGHT	20	30.0	14.7	13.6	18.8	19.3	17.9	12.2
	GAIN	20/8	27.4	13.7	14.6	14.9	21.2	19.9	14.0
	(cm)	8	17.6	16.1	6.2	6.8	4.5	9.4	6.3
v)	INITIAL	20	21.7	45.6	22.1	26.9	27.8	28.6	23.4
	HEIGHT	20/8	21.9	44.2	22.6	27.2	28.6	29.1	23.1
	(cm)	8	21.3	44.2	22.0	26.9	27.3	29.7	23.1
vi)	% INCREASE	20	138.4	30.9	61.5	69.9	69.5	62.5	52.2
	HEIGHT	20/8	125.2	32.2	64.7	54.7	74.0	68.5	60.7
		8	82.5	27.4	28.2	25.3	16.5	31.7	27.2

TABLE 3: 5b Levels of significance for growth stages.
** $p \leqslant 0.01$, * $p \leqslant 0.05$. (Tukey's test).

	CLONES	TEMPERATURE	PROGENY	TEMPERATURE
i)	**	20 20/8 8 **	AG KH CK AD HG **	20 20/8 8 **
ii)	**	20/8 20 8 **	KH HG AD AG CK **	**
iii)	**	**	*	**
iv)	**	*	*	20/8 20 8 **

FIGURE 3 : 3 Cumulative height gain of two Sitka spruce clones at three temperature regimes



3:4

3:5

Plate 3:4 Clone 8000 at 20°C, showing maximum extension growth, lateral shoot growth on leader and reflushing of some buds.

Plate 3:5 Clone 8000 at 8°C, showing less extension growth, well-formed terminal bud and pale green foliage.

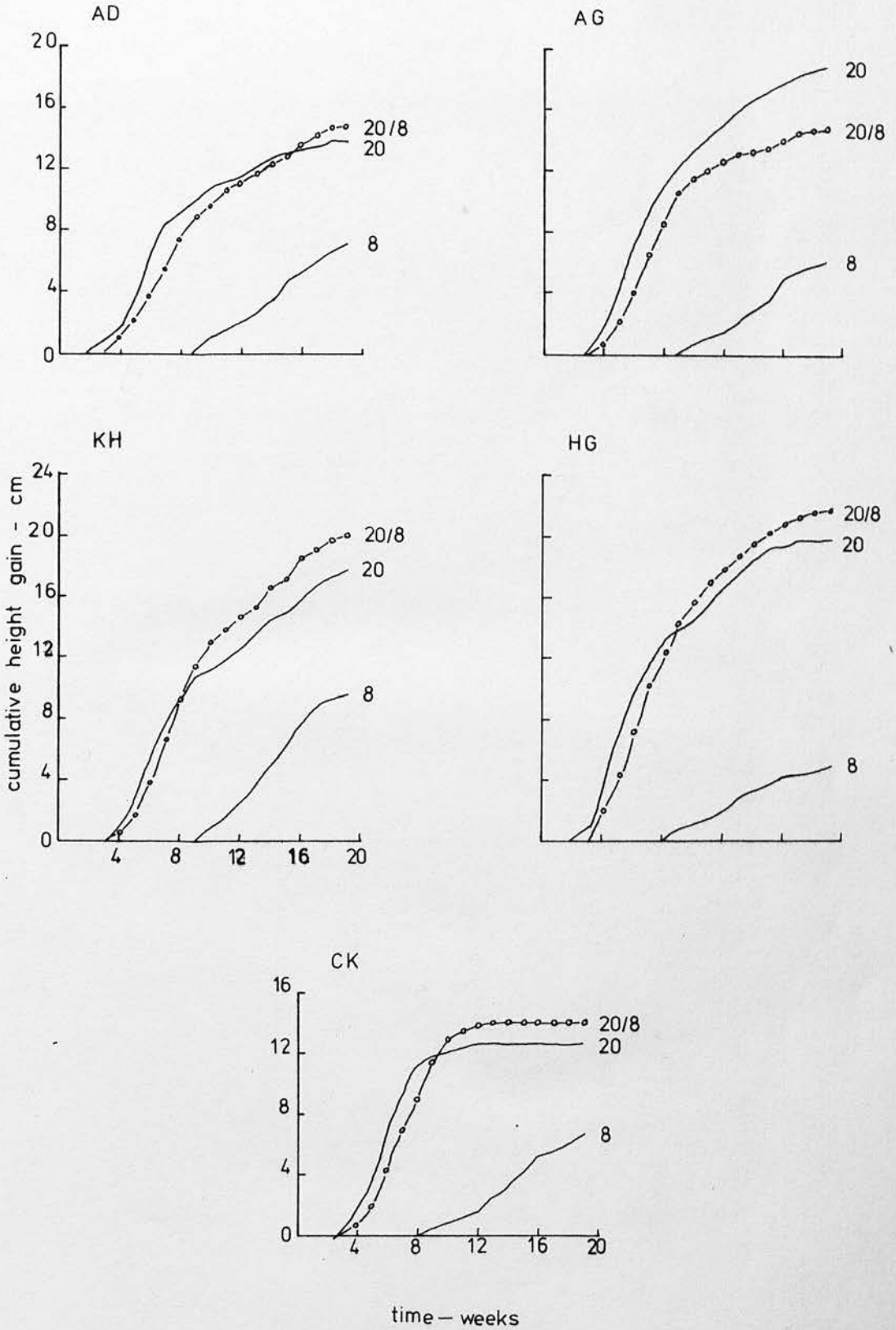
3:6

3:7

Plate 3:6 Clone 8014 at 20°C, showing poor extension growth, well-formed buds and dark green foliage.

Plate 3:7 Clone 8014 at 8°C, showing more leader extension growth than at 20°C and paler green foliage.

FIGURE 3 : 4 Cumulative height gain of Sitka spruce diallel cross progenies at three temperature regimes.



3:8

3:9

Plate 3:8 Progeny HG at 20°C, showing good extension growth of both leader and laterals, and many buds on leading shoot.

Plate 3:9 Progeny HG at 8°C, showing little extension growth, pale green foliage and close, short needles.

3:10

3:11

Plate 3:10 Progeny CK at 20°C, showing relatively poor extension growth (cf. progeny HG at 20°C).

Plate 3:11 Progeny CK at 8°C, showing poor extension growth, pale green foliage and close, short needles.

Table 3: 6. Parameter 'B' of the Gompertz equation as fitted to the growth data.

	Progeny				
	AD	AG	HG	KH	CK
20	0.355	0.303	0.318	0.219	0.728
20/8	0.285	0.422	0.327	0.289	0.573
8	0.269	0.292	0.352	0.330	0.291

highest values at 8°C.

The parameters A, B, C and M of the Gompertz equation, for each growth curve, were subjected to analysis of variance. The sum of squares (SS) due to fitting common B and M is labelled parallelism, and the SS due to fitting common A and C parameters is labelled displacement. Analysis of variance of these parameters showed both the parallelism and displacement mean square (MS) to be significant when compared to the within curves MS of 0.1725 (see below and Appendix 3), demonstrating that the curves are not parallel nor are they displaced equally.

Parallelism.

Source of variation	DF	SS	MS	VR	F 5%	F 1%
Progeny	8	44.920	5.615	32.55	2.01	2.65
Temperature	4	251.334	62.830	364.23	2.44	3.47
Interaction	16	25.850	1.630	9.45	1.72	2.15
Displacement						
Progeny	8	3699.089	462.386	2680.50	2.01	2.65
Temperature	4	5277.142	1306.785	7575.57	2.44	3.47
Interaction	16	427.390	26.712	154.85	1.72	2.15

The Gompertz equation appeared to fit the progeny growth curves adequately, but the fitted start and cessation of growth did not always correspond to that actually measured. The final height growth and duration of growth of any progeny still extending, is estimated in the fitting of the curve and the growth data recalculated as a percentage of the estimated asymptote. The parameter M for plants at 8°C was estimated to be about twice that at 20°C and 20/8°C, but height gain at the cessation of growth was estimated to be still significantly less than at the warmer temperatures (Table of C values, Appendix 3). The fitted curves therefore confirm the differences in growth at 8°C.

Although quite useful for providing overall comparisons of the curves, the Gompertz equation is of limited value when examining individual curve differences, as it provides no estimate of error and these comparisons are better made from the basic data.

Table 3:7 presents the relative height growth rate (RHGR) for each plant type, over the total period of the experiment. Clone 8000 grew faster than all other plant types at all temperatures, and although a different progeny shows a higher RHGR at each temperature, differences between progenies are small.

TABLE 3:7. Relative height growth rates of Sitka spruce at varying temperatures. ($cm.\ cm^{-1}.\ yr^{-1}$)

Clones

	8000	8014
20	$0.861 \pm .16$	$0.284 \pm .05$
20/8	$0.812 \pm .10$	$0.273 \pm .04$
8	$0.602 \pm .13$	$0.312 \pm .02$

Progeny

	AD	AG	HG	KH	CK
20	$0.477 \pm .13$	$0.528 \pm .16$	$0.515 \pm .26$	$0.476 \pm .15$	$0.435 \pm .15$
20/8	$0.485 \pm .17$	$0.438 \pm .09$	$0.552 \pm .10$	$0.532 \pm .37$	$0.475 \pm .06$
8	$0.212 \pm .03$	$0.273 \pm .09$	$0.161 \pm .03$	$0.276 \pm .03$	$0.238 \pm .05$

(Standard error confidence level = 95%)

The morphological variables measured at the end of the experiment are listed in Table 3:8a and Appendix 3. Temperature had no effect on the number of growth points; differences were accounted for by genotypic variation, the branches extending during the experiment from preformed buds.

Numbers of buds formed during the experiment however varied between temperatures and plant types. Significantly ($p \leqslant 0.01$) larger numbers of buds formed on the leader - subterminals and internodal buds - in the two warmer treatments (Table 3: 8b). Buds initiated on a current

TABLE 3:8a. Morphological variables measured at the end of the experiment.

		TEMP.	8000	8014	AD	AG	HG	KH	CK
i)	NO. GROWTH POINTS.	20	23.8	69.2	52.6	44.8	45.0	55.0	31.6
		20/8	28.8	66.6	52.6	45.2	44.0	57.0	37.3
		8	16.8	74.8	52.4	45.6	43.0	58.8	43.4
ii)	TOTAL NO. BUDS ON LEADER.	20	20.5	14.2	11.4	14.6	15.2	11.0	9.6
		20/8	17.0	13.8	11.6	10.4	18.2	11.2	9.6
		8	7.8	10.3	4.2	3.6	1.1	3.8	3.6
iii)	RATIO LEADER /NO. BUDS	20	1.5	1.1	1.1	1.3	1.3	1.6	1.3
		20/8	1.6	1.0	1.2	1.4	1.2	1.7	1.5
		8	2.3	1.6	1.6	1.7	4.0	2.5	1.8
iv)	1973 LEADER DIAMETER (mm)	20	4.3	3.7	3.8	3.5	3.2	3.3	3.5
		20/8	4.0	4.2	2.9	3.4	3.1	3.6	3.7
		8	3.0	4.2	2.5	2.5	2.5	3.2	2.8
v)	EXTENSION /DIAMETER LEADER (10^{-2})	20	7.0	4.1	3.3	5.7	5.9	5.3	3.6
		20/8	7.0	3.4	4.9	4.4	7.1	5.3	4.0
		8	5.8	3.9	2.6	2.4	1.9	2.9	2.2
vi)	TOTAL NO. BUDS ON 1973 BRANCH	20	6.4	3.7	4.8	5.6	7.5	5.4	1.8
		20/8	5.9	5.0	7.1	5.7	8.0	6.8	1.9
		8	1.4	2.8	0.7	0.4	0.01	0.7	0.7
vii)	1973 BRANCH LENGTH (cm)	20	21.0	8.6	10.5	14.0	17.2	16.3	8.4
		20/8	20.4	10.3	13.5	14.2	16.2	16.7	10.5
		8	11.0	9.5	5.1	5.1	5.0	6.2	5.1
viii)	DRY WT. 1973 BRANCH (g)	20	0.69	0.29	0.36	0.54	0.54	0.70	0.29
		20/8	0.59	0.51	0.68	0.68	0.68	0.95	0.47
		8	0.34	0.50	0.25	0.20	0.19	0.35	0.24
ix)	NEEDLE LENGTH (cm)	20	1.7	1.7	1.4	1.7	1.7	1.9	1.5
		20/8	1.7	1.6	1.6	1.8	1.9	1.9	1.7
		8	1.8	1.7	1.4	1.2	1.3	1.6	1.2
x)	DRY WT. 100 NEEDLES (g.)	20	0.13	0.12	0.12	0.14	0.12	0.15	0.13
		20/8	0.12	0.16	0.19	0.20	0.19	0.25	0.21
		8	0.24	0.34	0.23	0.19	0.18	0.37	0.21

TABLE 3:8b. Levels of significance of morphological variables. ** $p \leqslant 0.01$. * $p \leqslant 0.05$. (Tukey's test).

	CLONES	TEMPERATURE	PROGENY	TEMPERATURE
i)	* *	ns	KH AD AG HG CK **	ns
ii)	* *	20 20/8 8 **	ns	20 20/8 8 **
iii)	* *	20 20/8 8 **	KH CK AG AD HG **	**
iv)	ns	*	ns	**
v)	* *	ns	*	20 20/8 8 **
vi)	*	20 20/8 8 **	HG KH AD AG CK **	20 20/8 8 **
vii)	* *	20 20/8 8 **	KH HG AG AD CK **	20 20/8 8 **
viii)	*	ns	KH AG HG AD CK **	20 20/8 8 **
ix)	ns	ns	KH HG AG CK AD **	**
x)	* *	20 20/8 8 **	KH CK AD AG HG **	20 20/8 8 **

season branch were most frequent at 20/8°C in all plant types, except for clone 8000 (20°C). In every case except HG this corresponded to the longest current season branch length, and ratios of buds per unit branch length were similar at 20° and 20/8°C, for each plant type. CK produced very few buds.

Dry matter production was reduced at 8°C compared to the two warmer treatments. 1973 branch weight was related to branch length in all plant types except HG, where the largest branch weight at 20/8°C differed from the longest branch at 20°C. Temperature had no significant effect on branch weight in the clones, but was evident in needle dry weight ($p \leqslant 0.01$). Low temperatures decreased branch dry weight, but needle dry weights tended to be greater at 8°C. Temperature had no effect on the length of needles between clones, but differences ($p \leqslant 0.01$) are seen in the progeny.

A visual assessment of the comparative growth forms of all plants studied, was also made at the end of the experiment.

Needle colour at 8°C was a yellower green for all Sitka spruce plant types than at either of the warmer treatments. Clone 8000 tended to have yellow green needles under all treatments.

Needle widths were not measured, but a general trend in increasing width with decreasing temperature was seen. Needles were narrow in form at 20°C, thicker and closer together at 8°C (Plate 3:12).

The state of the terminal bud varied with treatment

Plate 3:12 Leading shoot of progeny CK at 8°C, showing close, thick needles.

and between progenies and clones. At 8°C all terminal buds had set, except for those of CK and AD which were still extending. At 20/8°C the majority of the progeny had terminal buds set or the needles at the tip of the leader were curling, indicating the slowing down of growth. All plants of clone 8014 at 20/8°C had obvious terminal buds, whereas clone 8000 were still extending. This continuous growth of clone 8000 at 20/8°C contrasted the growth state of 8000 at 20°C, which although extending was after a re-flush (Plate 3:4). An obvious change in the form and spacing of the needles on the leading shoot of these reflushed plants could be seen. The majority of the progeny and clone 8014 at 20°C had set bud, although a few plants were still extending, and 2 plants of 8014 and one plant of KH had reflushed.

The state of the branch buds followed similar trends to the terminal buds - all set at 8°C, various stages from extending to bud set at 20/8°C and 20°C.

3:5 Discussion.

Temperature effects on flushing.

The promotion of flushing under the warm temperature regimes agrees with the findings of Burley (1966a) and Caldwell (1971) for Sitka spruce. The start of flushing was retarded and the duration of flushing extended for all plants at 8°C. The lack of any differential growth at 20° and 20/8°C suggests that a day/night temperature differential is not necessary for flushing.

No clear response to temperature in the distribution

of bud break was observed, in contrast to that seen with Sitka spruce grafts (Caldwell 1971). These results may indicate a change in hormonal balance or sensitivity to temperature with the age of the plant material. Indeed, the majority of the plants at 8°C in this study (excepting 8014) flushed from the base upwards, whereas Caldwell found the opposite.

The differences seen in the mode of flushing between the clones and progeny at the warmer temperatures have also been noted for Norway spruce (Zumer 1968). Large buds of trees in a natural stand were found to flush in the same manner as the clones, and smaller buds like the progeny. It is suggested for Norway spruce that these methods provide a form of protection against frost - large buds that elongate rapidly after flushing being protected by the scale cap, and smaller buds that do not have this protection flushing later. Whether this explanation is valid for the plants in this experiment will be more obvious after examination of their flushing in the field (Chapter 4).

The clones flushing response under all three temperature regimes was advanced in comparison to the progeny (excepting HG). Clone 8014 began flushing before clone 8000 at all temperatures, but total duration of flushing was longer. It is possible that the difference in age of these clones may be involved in the duration of flushing. Neither clone showed any response to temperature in the order of flushing, exhibiting opposite sequences

under all treatments, indicating that this feature may be under genetic control. The earlier start and longer duration of flushing in clone 8014 is reflected in the heat sum required and it would seem that 8014 requires a larger energy input for full flushing.

Low temperature delayed every stage of the flushing of the progeny. The individual genotypes were indistinguishable at the start of flushing, but as flushing progressed the various genotypes exhibited differing responses. For each cross flushing was most rapid at 20°C, then 20/8°C and finally after about twice the number of days, 8°C. The order of the progeny in rate of flushing was consistent at each stage, but the response to heat sum varied, with the exception of HG which had the lowest requirement at each temperature. These results for vigour agree to some extent with those of Samuel et al.(1972), who show the superiority of parent H. The response of CK at 8°C with regard to heat sum for flushing, is in accordance with the field results that show CK to be superior under extreme conditions (R. Johnstone, pers. comm.).

Temperature effects on shoot extension.

The 'shoot' extension of Picea species depends upon the elongation of the preformed bud. The size of the terminal bud in Sitka spruce has been shown to be related to the amount of height growth (Burley 1966b) and thus from observations in this experiment, one would expect more growth from the clones, which had larger terminal buds than the progeny. This was true for clone 8000 but not

8014 whose height growth was surpassed by AG, HG and KH at the warmer temperatures. The potential growth of clone 8014 responded more to a cool temperature regime. It is unfortunate that some definite measure of bud size was not made.

Reciprocally, seedling height has been shown to influence the size of the terminal bud and the amount of height growth (Burley 1966b for Sitka spruce; Hellum 1967 for white spruce). Burley (1966b) found larger seedlings produced larger terminal buds for at least the first 2 years, so creating a height differential. The initial heights of the progeny seedlings varied, reflecting earlier differences in growth rate, according to the vigour of the genotype, and these differences were evident to some extent in the height gain achieved by the end of the experiment:

Initial height	KH	HG	AG	CK	AD
Height gain	KH	HG	AG	AD	CK
	decreasing height ⟶				

An advantage of using RHGR to compare the performance of plants is that it removes any effect of initial plant height.

Temperature during the growing season can modify the extension of the stem units in the preformed bud (Heide 1974b), and has been confirmed in this experiment. The closeness of the needles at 8°C indicates less extension than at warmer temperatures. Unfortunately needle numbers per unit length of current leader were not measured, in order to support this assumption. 8°C is considered

suboptimal for the growth of Sitka spruce [net photosynthesis optimum temperature = 19°C (Neilson et al. 1972), optimum temperature for height growth = 18°-24°C (Brix 1972)], and this appears to be so for most of the plant types investigated here. It is unlikely that the two progeny (AD and CK) that were still extending at the end of the experiment, would have achieved equivalent height growth to that observed at the warmer temperatures. The low 'C' values of the Gompertz equation for total height gain at 8°C, agree with this supposition (Appendix 3).

The ability of the various plant types for 'free' growth at the warmer temperatures was evident. Only clone 8000 at 20/8°C was still extending at the end of the experiment, with no sign of slowing down. Other plant types showed semi-indeterminate growth, in that growth had slowed followed by a reflush, during the course of the experiment. Clone 8000 (1 yr cuttings) was the most consistent in its ability for continuous growth. Clone 8014 (2 yr cuttings) at 20°C had two plants reflushed. The two-year old progeny showed varying abilities for continuous growth - a total of three plants at 20°C still extending, and one reflushed. CK and HG showed no potential for indeterminate growth. These results for two year plants agree with the findings of Nienstaedt (1966) for white spruce.

In general the growth response of Sitka spruce to temperature in this experiment agrees with the findings of

other workers. Genetic variation presumably accounts for observed differences in optimal temperatures. The beneficial effect of a day/night temperature differential as found by Brix (1972), was apparent for most of the progeny, but the effect was slight and not significant statistically. Mergen et al.(1974) concluded that Sitka spruce was not greatly dependent on a day/night temperature differential, and the results of this experiment are in line with this conclusion. The maximum growth of clone 8014 at 8°C, agrees with the findings of Caldwell (1971) for Sitka spruce grafts. From the results of Nielson et al. (1972), one would expect the mesophyll resistance at 8°C to be considerably higher than at 20°C, causing a reduction in net photosynthesis. It may be that clone 8014 is less adapted to the increased respiration demand at high temperatures.

It is generally recognised that duration of the growth period is the major factor affecting total height growth in conifers (Aldhous 1962). Since final height growth is largely predetermined, duration of growth must be a function of growth rate. Low temperature reduced growth rate considerably, especially in the progeny, but as stem unit expansion at 8°C was also reduced, duration of growth at 8°C was generally shorter. It is unfortunate that some plants were still extending at 8°C at the end of this experiment, and their final height gain was not known, but these values may be estimated from the fitting of the Gompertz equation.

One of the advantages of using the Gompertz equation is that it can estimate the final height gain, but its disadvantages include the inability to detect any reflushes of growth (as seen in KH). As a method for discerning inherent variation within a species it is most effective.

With regard to heat sum, most plants showed maximal growth at a daily heat sum $\geqslant 5^{o}C$ of $276^{o}h$ (i.e. $20/8^{o}C$). An optimum daily heat sum of $360^{o}h$ (constant $20^{o}C$) shown by other genotypes, is the same as that found by Mergen et al.(1974) for Sitka spruce. They however concluded that Sitka spruce is responsive to daily heat sum regardless of temperature fluctuations, a reflection of the equable diurnal and seasonal climatic patterns within the natural range. An interesting statistical approach, stability analysis, by Mergen et al. allowed the identification of adaptable provenances that react positively to environmental changes.

To some extent the differences in amount of current season branch length of the progeny, reflect differences in height growth as described by Cannell (1974). Longer branches subtend longer leaders and effects of temperature on leader extension are also evident in branch length. Bud formation in this experiment was severely reduced at low temperatures. Consequently, the ratio of number of buds per unit shoot length is greater at $8^{o}C$, especially for branches.

Branch dry weight is greatest at $20/8^{o}C$ for the majority of plants, which generally coincides with maximum

stem diameter measurements, and maximum branch lengths. Brix (1972) found temperatures of 18°-24°C optimal for diameter growth and dry matter production, in Sitka spruce seedlings.

Needle dry weights however tend to be greater at 8°C, indicating that at cooler temperatures a greater percentage of dry matter is retained in the leaves and augments the observation that needles at 8°C appeared thicker.

The lack of any difference in needle length of the clones under the three treatments and the obvious difference in dry weight of the needles, indicates a difference in needle shape (transverse section) with temperature. In the progeny, temperature affected the individual genotypes to different extents, resulting in varying ratios of dry weight to length of needle.

Having discussed the effects of temperature seen in this experiment, the pre-histories of the plants used should be considered, since the importance of conditions during bud maturation, the previous season on subsequent flushing and shoot growth has been stressed in the literature review, (3:1).

Both Sitka spruce clones showed signs of lammas growth, after being kept in a greenhouse until September 1972, and because of this the terminal portions of some leaders and branches bore pale needles and did not appear to have fully hardened buds. The time for bud maturation in these plants would have been reduced, if new buds had

to be differentiated, and this could result in less shoot extension the following year. However, without any fully-hardened clonal material for comparison no conclusions can be drawn.

Some of the progeny stored in a cold room at 2°C for about 8 weeks, appeared less healthy than plants under natural conditions. Brown 'spots' were evident on the needles of most plants and HG and AG especially looked weak. HG gave the appearance of being frosted and had the highest mortality rate during the experiment. It has been suggested that parent tree H could well have suffered frost damage, and progenies from tree H have been shown to continue growth for a longer period than progenies from other parents (Samuel et al. 1972).

Similar effects of cold storage at 4°C have since been reported for 1 year Sitka spruce seedlings, subsequently grown in a growth chamber (Buckley & Lovall 1974). After periods of 5-20 weeks in store, seedlings showed a significant decrease in survival and a decline in vigour, effects that increased with storage period. This illustrates the need for care in choosing plant material for experimental studies, and questions the usefulness of cold storage.

3: 6. Conclusion.

The results of this experiment show that different current temperatures markedly affect the rate and duration of extension growth in Sitka spruce.

A noticeable feature of the results is the variability

between genotypes in response to the temperature treatments, as indicated by the parameters calculated for the Gompertz equation.

The warmer treatments clearly accord with the suggested optima for photosynthesis (Nielson et al. 1972) and dry matter gain (Brix 1972) for Sitka spruce so that little would be gained from investigating a wider range of temperatures, but it would be interesting to follow up the marked differences in plant morphology between 20°C and 8°C treatments.

The superiority of the 20/8°C treatment and the small difference from 20°C, provides a useful criterion for the programming of controlled environmental regimes, in either the production of experimental plants or the glasshouse production of commercial stock.

CHAPTER 4. THE SEASONAL GROWTH OF SITKA SPRUCE IN THE FIELD AND ITS RELATION TO THE CLIMATIC ENVIRONMENT.

4: 1. Literature review.

In addition to the study of the effects of temperature in a controlled environment on the vegetative growth of Sitka spruce, the opportunity was taken to follow the growth of similar plants in the field, in conjunction with the collection of climatic data.

The principal environmental factors measured in this study were:- air temperature, precipitation, humidity, wind, solar radiation and soil temperature. In the natural environment these and other factors are interrelated, so that a change in one factor is usually accompanied by changes in one or more other factors.

The amount of apical growth in conifers is determined largely by the growing conditions of the previous summer (see Chapter 3:1), but here only the effects of the current season will be considered.

Temperature has been shown to be one of the dominant current season factors controlling the vegetative growth in a number of species. Temperature effects on specific phases in the vegetative growth cycle have been studied. Growth and development of buds of Norway spruce in a natural stand followed maximum temperature fluctuations, with growth retardation during cold weather periods (Zumer 1968). Similar results for bud burst were found in white spruce (Fraser 1962). There is evidence that spring flushing in Picea spp. is related to a temperature

threshold of about 5°C (Roche 1969). Once this threshold is reached the probability of lethal frosts is decreased. Freezaillah (1974) noted that the flushing of Sitka spruce seedlings in 1972 and 1973, started when the mean weekly air temperature was about 6°C, though on different dates. Dahl & Mork (1959) concluded that the main phase of growth in Norway spruce is controlled by the effect of temperature on respiration, with daily shoot elongation correlated to the mean temperature of the six warmest hours of the day.

The effect of daylength on the seasonal growth of conifers is reviewed in Chapter 5, but it is necessary to point out here that daylength also influences air and soil temperatures. Air temperature is immediately influenced, but temperature below the soil surface is subject to a lag effect, because heat is conducted slowly in the soil. Length of day has been shown to largely determine the difference between mean daily air and soil temperatures, throughout the season (Millar 1965).

The effect of soil temperature, in the field, on shoot growth in conifers is not well documented. Rooting-medium temperature and saturation vapour pressure deficit (SVPD) variables dominated the growth-climate relationship of Sitka spruce seedlings in the field (Freezaillah 1974). Spring maximum soil temperatures were considerably lower than air temperatures and reduced with depth.

The importance of rainfall, is seen not only in

the annual amount, but also in the seasonal distribution and frequency of precipitation. Considering the climatic environment at the place of origin of Sitka spruce, it is likely that moisture supply will be an important factor influencing the vigour of this species in Britain.

For Sitka spruce increasing SVPD resulted in a linear increase in leaf diffusive resistance and in a growth study, an increase from 3.5mb to 10.6mb reduced current shoot growth from 2.05mm day^{-1} to 1.5mm day^{-1} (Grace et al. 1975).

Wind is an important component of upland climate and Sitka spruce is planted up to elevations of 500m above sea level in Scotland. The height of Sitka spruce seedlings at an altitude of 480m, was shown to be 25 per cent less than the height of seedlings at 230m (Freezaillah 1974). The difference of wind run between these two altitudes was involved in this response. The physiological response to wind was investigated in a wind tunnel by Grace et al. (1975). No marked changes in transpiration occurred over a range of windspeeds from 0.01 m^{-s} to 4.0 m^{-s}, suggesting that the effect of wind is likely to be due to cooling.

Species are known to vary not only in the amount of light they require at different stages of growth, but also in their growth response to different levels of light intensity. Some species are known to show optimal height growth under light intensities of less than 100 per

cent (Logan 1969). A study by Fairbairn & Neustein (1970), of the responses of several conifer species to varying light intensities in a nursery, recorded increase in shoot and root length and dry weight for Sitka spruce, up to full light. In a growth room study, an increase in light intensity from 450 to 1000 ft.c. had no effect on the height growth of Sitka spruce seedlings, although dry matter production and stem diameter were greatly increased (Brix 1972).

Care must be taken when comparing the response of plants to different light intensities grown in a nursery or growth room, to those under natural field conditions. In natural plantings some shading could be beneficial, through its effect on leaf temperature and soil surface temperatures. Also growth responses to shading in controlled experiments where plants are irrigated, may bear no resemblance to the growth of plants in the field, where soil moisture conditions might be limiting.

4:2. Materials and Methods.

1) Establishment of climatic station.

A climatic station was set up in the nursery at the Forestry Commission, Northern Research Station in April 1973, adjacent to four plots of 4 year old Sitka spruce diallel-cross progeny.

2) Plant material.

The Sitka spruce progenies chosen for observation corresponded to those used in the first experiment (Chapter 3) in the growth rooms, namely AD, AG, HG, KH, CK.

The complete Sitka spruce progeny trial (Samuel et al. 1972) had been randomly planted in 1970, in 4-plant line plots at 2m x 2m spacing, in 3 of the 4 main plots (see plan, Appendix 4). A total of 12 trees per cross were measured during the growing season. Ten Sitka spruce clone 8000 and eight Sitka spruce graft 1054 (Glenfinart), were re-potted in April 1973 and sunk into the nursery soil, in order to follow their seasonal growth characteristics.

From May onwards the potted Sitka spruce clones and grafts were fertilised weekly. During June all plants were sprayed against aphids.

3) Measurements.

a) Climatic variables.

Temperature, solar radiation, rainfall and wind run data were collected from April to November 1973, by the methods and at the frequencies given in Table 4:1. The thermistor probes of the Grant temperature recorder had a range of -10°C to 40°C. The instrument was battery operated and recorded the temperatures at hourly intervals. Tube solarimeter (Szeicz et al. 1964) output was integrated by a coulometer and calibrated against a Kipp solarimeter. The length of the natural photoperiod was obtained from Meteorological Office tables.

Table 4:1. Summary of Climatic Measurements.

Variable	Frequency	Details
Temperature Air at 1.0 m) Wet bulb at 1.0 m) in radiation shield. Soil at 5, 10 and 20 cm depth. Plant pots at 5, 10, 20 cm depth.	Hourly.	Grants Miniature Temp. Recorder Model D. Interchangeable thermistor probes. All measurements in duplicate.
Rainfall mm.		Standard 12.7 cm rain gauge to the south of the plots.
Radiation cal. cm^2.	Weekly.	Tube solarimeter with coulometer. Measurements in duplicate, within plots.
Wind run miles/wk.		Cup counter anemometer, within plots.

b) Plant growth.

All plants were measured for the following:

initial height

time and sequence of flushing

weekly height growth —

from the base of the terminal bud in the progeny, and from a pre-marked point on the stem of the potted plants.

4) Analysis.

a) Climatic variables.

The climatic data was read off the Grant recorder charts onto forms and transferred to punch cards for computer analysis and summarising on a weekly basis. The variables computed and the symbols used for denoting

them, are listed below :-

Bucket temperature at 10 cm, ^{o}C.	B10
Soil temperature at 10 cm, ^{o}C.	S10
Air temperature, ^{o}C.	A
Minimum air temperature, ^{o}C.	AMIN
Accumulated air temperature, $\geqslant 5^{o}C$, degree-h.	ACCUMA
Saturation vapour deficit, mb.	SVD
Maximum saturation vapour deficit, mb.	SVDMAX
Rainfall	RAIN
Solar radiation	SOLRAD
Photoperiod	PHOTOP

These variables were analysed by Principal Component Analysis and the mean weekly height growth of the trees regressed against the extracted components.

b) Plant growth.

The data collected for flushing and height growth was subjected to analysis of variance, as in Chapter 3. The height growth curves were fitted by the Gompertz equation (see methods, Chapter 3), in order to assess the growth of the different genotypes in the field, and to compare the outdoor performance of the trees with that in the growth rooms.

The relative height growth rates (RHGR) of all progeny were calculated using the formula as in Chapter 3. Unfortunately, accurate measurements of the initial height of the clones and grafts were not made, therefore the RHGR of these plants could not be calculated.

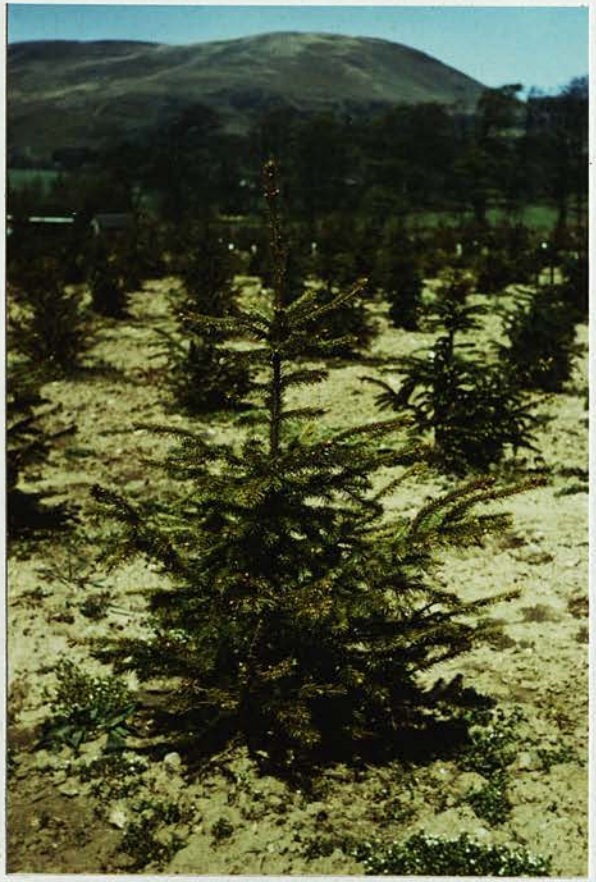
4:3. Results.

Flushing.

The swelling of buds was first observed in clone 8000 on 6.4.73 and this date was termed Day 1 in the analysis of flushing and height growth of all plant types. The buds of the progeny began swelling at the end of April, and the grafts by 7.5.73.

Table 4:2 shows the number of days until terminal bud flushing and total plant flushing. Clone 8000 was fully flushed about two weeks before all the other plant types and graft 1054 was the latest to flush. Of the progeny, HG was well advanced and was the only progeny that tended to flush from the terminal downwards (Plates 4:1 and 4:2). This relatively early flushing and the sequence of flushing may be partly responsible for the number of damaged terminal buds in this cross - three terminals out of the 12 trees did not flush. The majority of the remaining progeny flushed from the base upwards, with often the sub-terminals last to flush (Plate 4:3). The progeny did not show any consistent mode of flushing. Some buds retained scale caps (Plate 4:3), while in others the needles appeared through a gap in the top of the bud. Both modes could be seen on some trees. Eight days separated the progeny at total flushing ($p \leqslant 0.01$) and about seven days in duration of flushing. The progeny first to flush was not necessarily the fastest.

4:1



4:2

Plate 4:1 Progeny HG - whole tree, swelling thoughout with some lower buds flushed (15.5.73).

Plate 4:2 Progeny HG - leading shoot, fully flushed. Terminal bud needles extending through gap in bud scales (15.5.73).

Plate 4:3 Progeny AD - leading shoot and top whorl. Flushing from the base of the tree upwards, some buds with scale caps (15.5.73).

TABLE 4:2. Time (days) to terminal bud flushing and total plant flushing. (Day one = 6.4.73)

		8000	1054	AD	AG	HG	KH	CK
i)	TERFIN	39.7	57.4	54.7	52.8	46.8	55.5	57.4
ii)	TOTFIN	40.6	58.8	56.8	53.5	50.4	57.3	58.3
iii)	SEQFIN	0.9↑	1.5↕	2.08↑	2.09↑	2.67↓	0.80↑	0.83↑
iv)	DURATION OF TOTAL FLUSHING	40.6	27.0	33.8	30.4	27.4	27.1	29.3

Levels of significance for stages of flushing. ** $p \leqslant 0.01$, * $p \leqslant 0.05$. (Tukey's test).

	8000 1054	PROGENY
i)	**	CK KH AD AG HG **
ii)	**	CK KH AD AG HG **
iii)	ns	ns

Height growth.

As only eight days separated the progeny in flushing, no significant differences in the start of extension growth were seen. (Table 4:3). Analysis of variance shows progeny HG to have a significantly longer growing season than the other progeny ($p \leqslant 0.01$). This result is due to a second flush of lammas shoots in five of the nine trees measured. The analysis however, only partly takes into account this reflush, nine weeks after the initial flush, which accumulated 2.8 cm. more growth over a period of five weeks. Progeny AG combined a relatively long growth period with the greatest shoot extension. Shoot extension in progenies CK, AD and KH began and finished at similar times, but the amounts of growth made varied with

genotype, (Figure 4:1). Looking at the cumulative percentage growth all progeny except HG completed 90% of their height growth after 6-7 weeks, whereas HG took 11 weeks.

TABLE 4:3. Growth stages (weeks) and height gain - from analysis of variance.

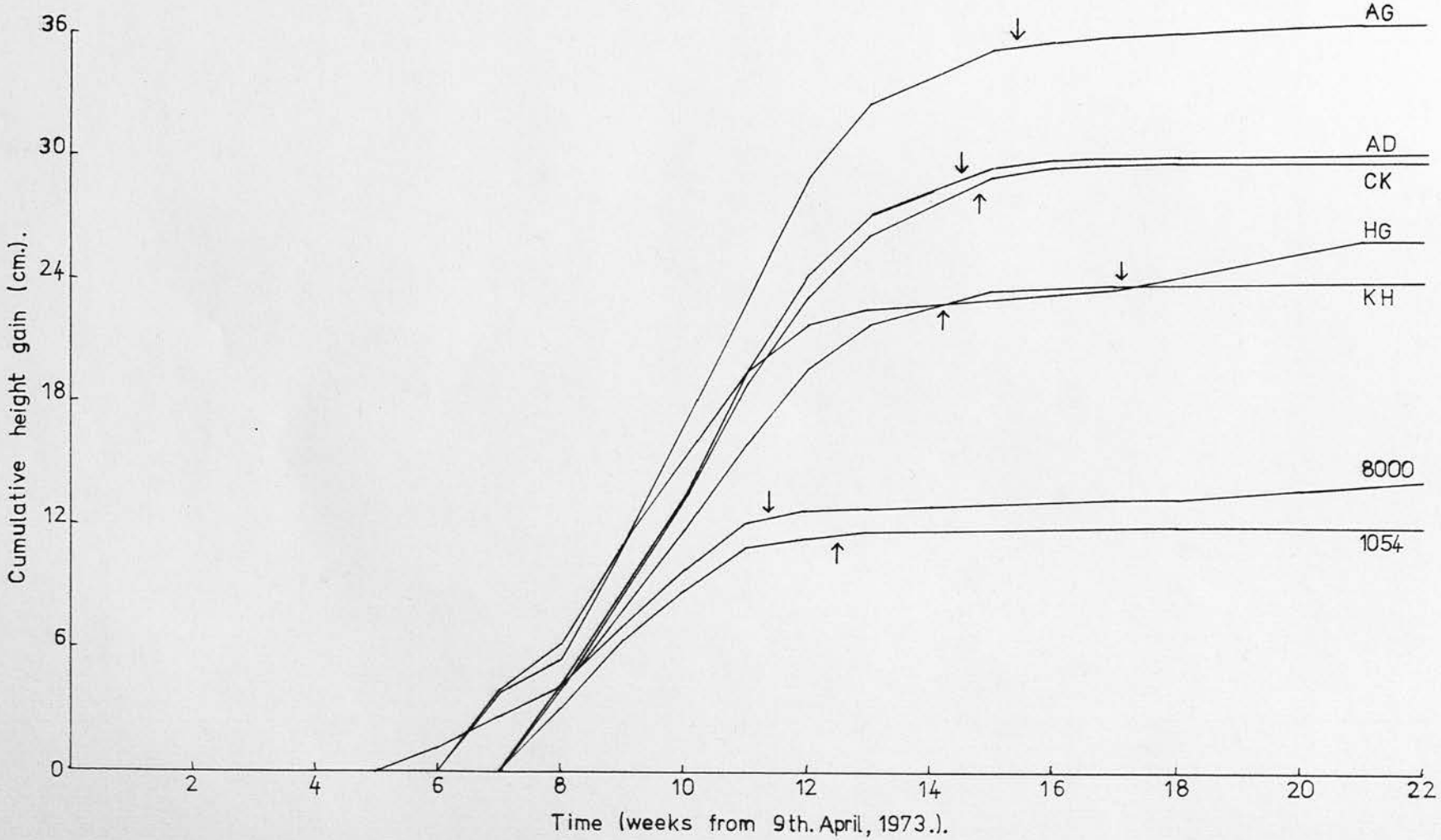
		8000	1054	AD	AG	HG	KH	CK
i)	START GROWTH	6.0	8.0	8.0	7.0	7.0	8.0	8.0
ii)	END GROWTH	11.4	12.5	14.5	15.4	17.1	14.2	14.8
iii)	DURATION GROWTH	5.4	4.5	6.5	8.4	10.1	6.2	6.8
iv)	INITIAL HEIGHT (cm)	ca.25.0	-	87.5	105.8	96.2	110.4	92.0
v)	HEIGHT GAIN (cm)	14.5	11.8	30.3	37.0	26.1	23.8	29.7
vi)	% INCREASE HEIGHT	-	-	34.6	35.0	27.1	21.6	32.3

Levels of significance for growth stages
** $p \leqslant 0.01$ * $p \leqslant 0.05$ (Tukey's test).

i)	ns						ns
ii)	**	KH	AD	CK	AG	HG	**
iii)	*	KH	AD	CK	AG	HG	**
iv)		not analysed					
v)	ns	KH	HG	CK	AD	AG	*

Both the clones and the grafts had shorter growing seasons than the planted trees. With an early start to shoot extension clone 8000 was the first plant type to cease growth. Once again however, the analysis of variance misses the reflush of four of the ten clones by week 18, which achieved a mean increase in height of 1.2 cm.

FIGURE 4 : 1 Cumulative height gain of Sitka spruce in the nursery , 1973. Arrows denote end of main growth period.



The relative height growth rates of the progeny are shown below (Table 4:4). Progeny AG which accumulated the greatest height gain has the highest RHGR, and the other progeny follow similarly with the lowest RHGR equalling the poorest height growth (KH).

TABLE 4:4. Relative height growth rate* of Sitka spruce progeny in the nursery. ($cm.cm^{-1}.yr^{-1}$)

	AD	AG	HG	KH	CK
RHGR	$0.288 \pm .04$	$0.305 \pm .03$	$0.269 \pm .05$	$0.173 \pm .07$	$0.269 \pm .04$

Parameter B of the Gompertz equation as fitted to the growth data, is listed in Table 4:5 for each progeny and for the potted plants.

TABLE 4:5. 'B' Parameters from the Gompertz equation.

	AD	AG	HG	KH	CK	8000	1054
B	0.566	0.505	0.508	0.544	0.539	0.570	0.819

Parameter B represents the slope of the curve and it can be seen that of the progeny, AD and KH display the fastest rates. The variation in this parameter confirms that each genotype is functioning differently in the same environment. Clone 8000 shows a slightly higher growth rate than the progeny, while graft 1054 exhibits a fast rate over a short period of time.

Data available for the height growth of the progeny during 1971 and 1972, (R. Johnstone pers. comm.) is presented in Table 4:6. It can be seen that the order of the progeny with decreasing height growth varies from year to year, but overall AG shows the most extension growth and HG the poorest.

* 95% confidence interval

TABLE 4:6. Comparison of extension growth of progeny over 3 years. Mean of 12 trees/progeny.

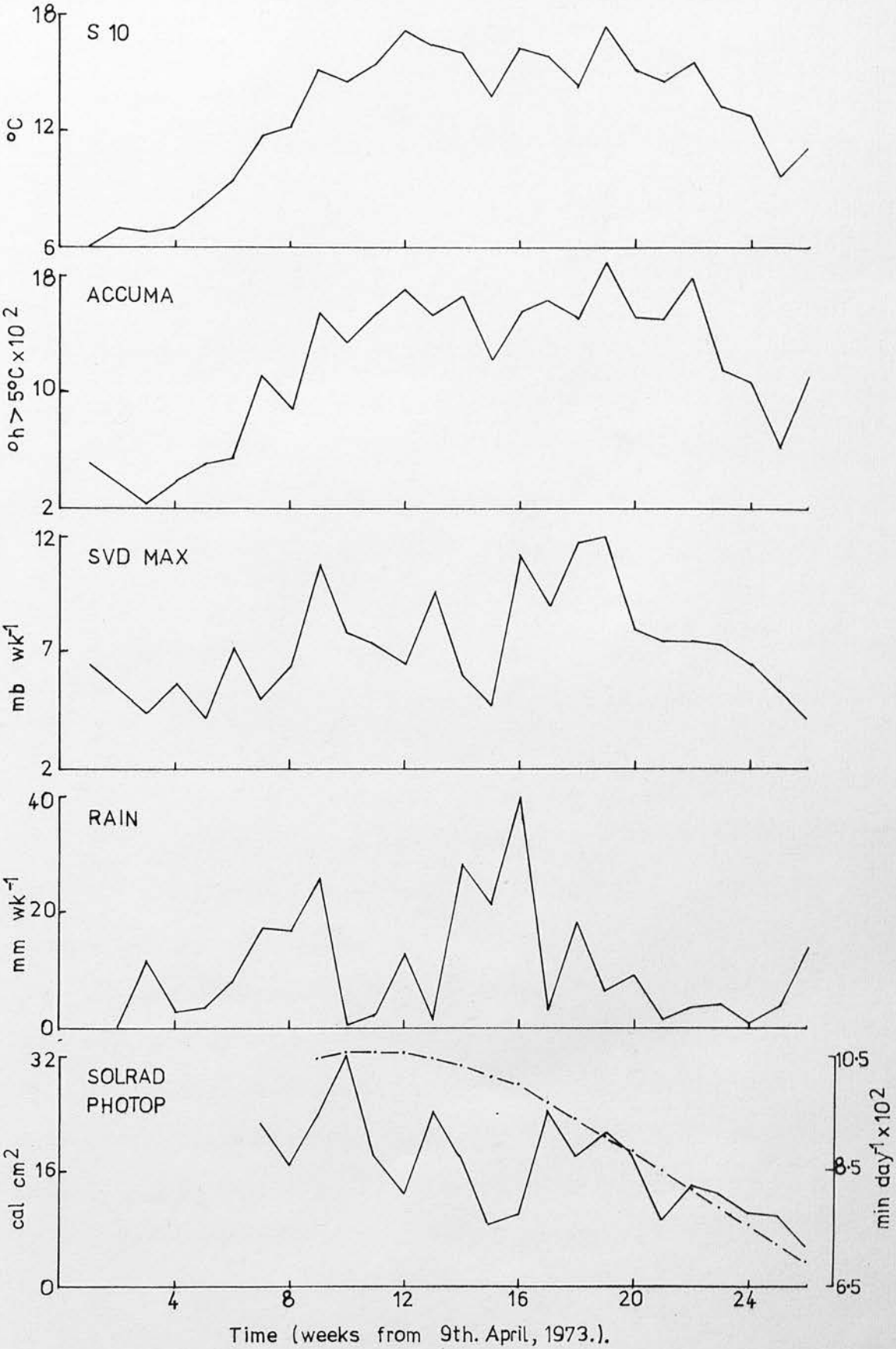
Height Gain - cm.	AD	AG	HG	KH	CK
1971	21.0	30.29	25.33	33.21	25.79
1972	22.74	23.17	19.01	24.09	28.82
1973	30.3	37.0	26.10	23.80	29.70
Σ	74.04	90.46	70.44	81.10	84.31
$\bar{x}$	24.68	30.15	23.48	27.03	28.10

Height growth - climate relationship.

The monitoring of climatic conditions during the experiment was fairly successful. The collection of temperature data was achieved throughout the season, but failure to measure wind run and solar radiation consistently, reduced the number of weeks with full quotas of climatic variables to 14, beginning at week 9. (Figure 4:2).

The principal component analysis of the climatic variables measured during the course of the growing season, indicates the most important factors influencing shoot growth. In this analysis a correlation matrix is calculated from the standardised data and the eigen values and eigenvectors are extracted. The vectors form components which are uncorrelated with one another and the variability of the data can often be largely accounted for by the first few components. By examining the 'weightings' of vectors on the components, the main sources of variation may be interpreted. Components with

FIGURE 4:2 Comparison of climatic data.



eigenvalues of less than 1.00 can be ignored, and with the largest vector scaled to a value of 1.00, vectors with values less than $\pm$ 0.7 are rejected.

Table 4:7 gives the weighting of the original variables in the computed components for weeks 9-23 (28 May - 10 Sept.)

TABLE 4:7. Weighting for original variables in computed components of climate.

Variable	Components 1	2	3	4
B10	-.4348	.0760	-.0095	-.0851
S10	-.4278	.0018	-.1049	-.1792
A	-.4513	.0632	.0301	.0997
AMIN	-.3045	.3806	.0534	-.0116
ACCUMA	-.4502	.0712	.0170	.1243
SVD	-.2180	-.4900	.0788	.2224
SVDMAX	-.1967	-.4735	.1609	.3267
WIND	.1143	-.4705	.1435	-.1171
RAIN	-.1206	-.1854	.5802	-.4752
SOLRAD	-.0906	-.2901	-.6906	.0766
PHOTOP	-.0824	-.1902	-.3443	-.7305
Eigenvalue	4.6962	2.7653	1.3050	1.2652
% variation accounted	43	25	12	11

It is clear that measures of temperature, both soil and air, are strongly represented in the first component. The second component is associated with humidity (SVD) and wind, the third a contrast between solar radiation and rain and the fourth represents photoperiod.

Results of the regression of the components against the mean weekly height growth of the progeny and clone

8000, are shown in Table 4:8.

TABLE 4:8. Percentage reduction in variation of extension growth due to the computed components.

Component Interpretations.	AD	AG	HG	KH	CK	8000	$\bar{x}$
1. Temperature.	1.49	0.62	.004	0.75	0.92	0.49	0.71
2. SVD, Wind.	1.06	0.06	0.33	3.10	1.32	0.12	0.99
3. Solrad. V. rain.	27.89	36.73	51.00	30.02	29.14	39.30	35.68
4. Photop.	39.55	37.14	11.63	33.25	43.28	10.35	29.2
5. Wind.	0.13	0.23	0.89	1.18	0.28	2.84	0.92
6. Amin.	5.66	8.20	5.13	2.72	4.11	2.56	4.73
7. Photop, solrad.	5.03	0.41	3.44	7.01	4.08	5.55	4.25
8. Temperature.	0.74	3.00	12.38	0.58	1.17	18.59	6.07
9. SVD, S10.	12.86	2.55	6.91	16.89	10.43	9.02	9.77
TOTAL	94.41	88.94	91.71	95.50	94.73	88.82	

Components 3 and 4 of the climate apparently are the most important influences on extension growth and it can be seen that the different genotypes react differently to the climatic factors. The variation accounted for by these 9 components forms the greater proportion of the total variation, components 10 and 11 being of little account. The effect of wind appears insignificant, and SVD has a lesser influence than might have been expected.

4:4. Discussion.

Flushing.

The time of flushing of Picea species has been shown to

correspond to a certain threshold value of mean daily or weekly temperature (Roche 1969, Freezaillah 1974). Temperature recordings in the nursery began on 9th April, 1973, and the first day with a mid air temperature $\geqslant 5^{o}C$ was 13th April, 1973. Clone 8000 therefore responded to a lower critical temperature than the $5^{o}C$ or $6^{o}C$ reported previously.

The sequence of flushing within the plants followed recognised trends (Zumer 1968), in every case except HG. This pattern of bud break from the base of the tree upwards, allows the terminal shoot to avoid frost damage and it was noticeable that the terminals of progeny HG had been previously damaged. To discern whether this damage was caused by spring or autumn frosts is difficult, as not only was progeny HG prone to early flushing, but lammas growth at the end of the season left the terminal shoot unhardened and prone to frost damage in the autumn. Samuel et al. (1972) consider that parent H could have a southern origin, and confirm that progenies from tree H do continue growth for a longer period in autumn than progenies from other parents. Lines & Mitchell (1966) point out that spring frost damage is less likely to occur in trees in cultivated ground (as was the nursery), than to trees growing in grass, presumably due to the greater ease of heat transfer from bare soil.

The mode of progeny flushing was not related to bud size, as was suggested by Zumer (1968) for Norway spruce.

The period of flushing in the progeny did not vary greatly and the mean duration for all plants was similar to that obtained by Lines & Mitchell (1966), for Queen Charlotte Islands provenance seedlings in Bush nursery, in 1961.

The length of time for total flushing in the nursery, is similar to the 8°C treatment in the growth rooms (Chapter 3). The order of flushing duration among the progeny varies between nursery and growth room, the main difference being that KH ranked fourth at 8°C, compared to first in the nursery. The early flushing of progeny HG (totfin) in the nursery, is consistent with the performance in the growth room at 8°C. Only AD and CK responded to the artificial 8°C regime with a shorter flushing duration than in the field. The similarity between the 8°C results and the nursery supports the suggestion that a threshold temperature trigger for flushing exists.

At 8°C in the growth room, all progeny displayed an upward sequence of flushing. The reason for HG flushing downwards in the field is not clear, but may be concerned with thermoperiodism.

Flushing of clone 8000 in the nursery was considerably retarded in comparison to the growth room at 8°C, and was five times as long as at 20°C.

Height growth.

The completion of 90% of the height growth of most plant types by mid-July, agrees with the findings of Lines &

Mitchell (1966) that shoot extension growth occurs in a short part of the frost-free season. A similar date for 90% extension of Alaskan provenance seedlings in the same nursery, was found by Kraus & Lines (1976), although southern provenances grew on longer. This difference between the progeny and seedlings, may be a result of free growth by the seedlings.

The different genotypes made significantly different amounts of height growth. The RHGR for 1973 show progeny AG to be superior and progeny KH the poorest. A comparison of the height gain of 1973 to the two previous years, shows the trend between progenies to vary. AG consistently shows the most height gain and progeny HG ranks fifth over the three years. This poor result for HG in the field reflects the detrimental effect of frost, since with a long growing period it should achieve greater height growth. It is also interesting to note the difference between genotypes with a common parent.

Inherent differences in shoot elongation phenology, may reflect differences in the number of stem units laid down in preformed buds. However, Cannell et al. (1976) suggest that some genotypes may be predisposed to extend individual stem units more than others and that this may be inherited separately from factors affecting stem-unit number. The form of the trees in the nursery varied, some being more branched than others, which could affect the interception of solar radiation, and the photosynthetic

capacity of the genotype.

The extension growth of the four-year old trees in the nursery, is pre-determined to a large extent the previous year within the terminal bud. Comparisons therefore, with the height growth of two-year old seedlings in the growth room are not entirely valid, since the phenology changes with age. The seedlings in the controlled environment were still capable of 'free' growth.

Ranking of the progeny for variables such as duration of growth and RHGR, in the nursery and at 8°C, is shown below, and the different expression of the genotypes in the two environments is clear.

Duration of growth:	nursery	KH	AD	CK	AG	HG
	8°C	AG	AD	KH	HG	CK
RHGR :	nursery	KH	HG	CK	AD	AG
	8°C	HG	AG	CK	AD	KH

(increasing values ⟶)

Progenies of parent C were found to be superior in field conditions (R. Johnstone pers. comm.), but inferior in a glasshouse test (Samuel et al. 1972). This is not evident when comparing growth at 8°C with the nursery, possibly due to the similarity in total energy input of the two environments. However, CK's mean performance at all temperatures in the growth rooms was the poorest of the progeny tested.

The duration of growth of clone 8000 in the nursery

was shorter than for the progeny and only half that at 8°C in the growth room. In a controlled environment, clone 8000 had the longest growth period of all plants tested. In Chapter 3 it was suggested that clone 8000 may be capable of free growth, but this was not evident in the nursery. The tendency for a second flush is consistent in both environments however.

The growth pattern of graft 1054 in the nursery, is similar to that found for mature trees in British Columbia (Owens & Molder 1976), with elongation completed by mid-July. The growth of the potted plants in the nursery as compared to the planted trees, is obviously subject to the effect of a different rooting medium and consequent soil temperature and moisture conditions.

Height growth - climate relationship.

The principal component analysis indicates the main climatic factors influencing extension growth. Solar radiation, rainfall and photoperiod were found to be the main variables. Since this analysis used data from week 9 (early June onwards), it is not surprising that solar radiation and the related photoperiod should be important. Rainfall during the growth period was low, when compared to data for Bush nursery in years 1959-1961 (Lines & Mitchell 1966). Despite this low rainfall, the mean weekly SVD did not exceed 5mb, although the maximum SVD reached 12mb. These values are relatively low and are thus unlikely to have major effects on shoot extension. Wind was not an

important influence on extension growth, in agreement with the findings of Grace et al. (1975) in a wind tunnel.

Temperature was strongly represented in component 1, but the reduction in total variation due to component 1 was low. This result was somewhat surprising. Maximum air temperature has frequently been found to be important for height increment in young stands of Sitka spruce (Fraser 1970), and a strong dependence of height growth on temperature was seen for Sitka spruce seedlings (Freezaillah 1974).

The approximate dates of growth cessation (from Analysis of Variance) and the corresponding daylengths and mean weekly temperatures, are shown below :-

	8000	1054	AD	AG	HG	KH	CK
Date	28.6	5.7	19.7	26.7	6.8	17.7	21.7
Daylength (h)	17.5	17.0	16.7	16.4	15.7	16.9	16.7
Temperature (^{o}C)	14.0	14.9	14.5	14.7	14.1	14.5	14.5

It can be seen that temperature was not the limiting factor and illustrates the effect of decreasing daylength on seasonal growth. A similar result was obtained by Freezaillah (1974) - Sitka spruce seedlings ceased growth at the end of August, when mean weekly air temperatures were 14^{o}C. Photoperiodism is a dominant factor controlling growth, in agreement with the observations of Lines & Mitchell (1966).

CHAPTER 5 THE INFLUENCE OF TEMPERATURE ON THE CESSATION OF HEIGHT GROWTH OF SITKA SPRUCE PROVENANCES.

5:1 Literature Review.

The natural distribution of Sitka spruce along the coastal region of west North America has been detailed in Chapter 2. When a plant species occurs over a wide geographic range, populations growing in different localities frequently display differences in one or more traits. This phenotypic variation associated with locality may be due to environmental or genetic factors or interactions between them. Such ecotypes or varieties are commonly termed 'provenances', defined by Snyder (1959) as "the original source of seed or propagules".*

The study of provenance variation in tree species has received considerable attention and experiments have been conducted both in the field and in controlled environments to examine differences in such characteristics as flushing, height growth, growth cessation, the development of shoot apices and chilling requirements.

Photoperiodic responses.

The importance of decreasing daylength after midsummer in initiating the seasonal rest period in trees has been acknowledged in a number of reports (Kramer 1936, Downs & Borthwick 1956, Wareing 1956). The decisive factor in photoperiodism is the length of the longest uninterrupted daily dark period and the longest inhibitory daylength is termed the 'critical daylength'.

The common occurrence of photoperiodic ecotypes in

* but now taken to mean the actual place of seed collection.

Northern Hemisphere tree species with a large north-south range was demonstrated by Sylven (1940). Vaartaja (1959) tested the hypothesis of photoperiodic ecotypes in forest trees, using latitudinally distant seed sources and artificial photoperiods. He showed that the critical daylength for extension growth cessation in Sitka spruce was greater for a northern source (60°N), than for a southern source (43°N), and that the endogenous growth pattern was entirely overruled by the effects of photoperiod. This interaction between latitude of seed origin and photoperiod, substantiated the presence of ecotypes in this species.

Provenance trials of Sitka spruce have since confirmed the photoperiodic control of apical growth cessation (Aldhous 1962, Burley 1966b, Lines & Mitchell 1966, Pollard et al. 1975, Kraus & Lines 1976). Northern provenances when grown in the field in Britain, ceased growth while other environmental factors were still favourable (Lines & Mitchell 1966). The average date of growth cessation was also related to the latitude of the experimental site, with the longest growth period at the most northerly site, thus reinforcing the influence of photoperiod.

A field study of the seasonal growth of a complete range of Sitka spruce provenances, divided into groups by geographical regions, demonstrated the clinal pattern of earlier growth cessation with increasing latitude of the groups (Kraus & Lines 1976). Provenances south of

latitude 53°N however, were considered as parts of one population with respect to growth cessation and terminal bud formation. In contrast, provenances from Alaska showed variation in these traits unrelated to latitude, indicative of a heterogenous population.

Provenance seedlings from the same IUFRO* collection as those used by Kraus & Lines (1976), were subjected to artificially declining photoperiods in a controlled environment (Pollard et al. 1975). A four-hour difference in critical photoperiod between northern and southern provenances was found, ranging from 13h to 9h.

The time of bud formation in Sitka spruce is closely correlated with latitude of seed origin and in a nursery and glasshouse study extended over 120 days for year-old seedlings of 47 provenances (Burley 1966b). A similar result was obtained by Aldhous (1962), with three months separating time of bud formation in Alaskan and Oregon provenances.

Selection in the native habitat produces genotypes in which the length of the winter dormant period is adapted to avoid lethal frosts in autumn and spring. The selective advantage of a response to decrease in daylength is evident from the fact that daylength is the only environmental factor which changes in a consistent manner each year. Such an indirect adaptation to the environment is discussed by Vaartaja (1959). However, the onset of dormancy is correlated with climate and not

* IUFRO - International Union of Forest Research Organisations.

latitude alone (Burley 1966b), thus any variations in local environmental conditions may have an effect, resulting in a discontinuous pattern.

Roche (1969) found a clinal relationship between the altitude of spruce provenances and the degree of dormancy in British Columbia, with high elevation provenances entering dormancy earlier, while temperatures were still increasing. He considered the dormancy curve to characterise a provenance quite accurately. High-elevation ecotypes of Norway spruce were found to have longer critical photoperiods than low-elevation ecotypes from the same latitude (Heide 1974a).

The regulation of the seasonal growth cycle of Sitka spruce has received less attention than other coniferous species in which continentality and altitude of seed origin have been shown to influence the photoperiodic response (Vaartaja 1959, Irgens-Moller 1957).

Photoperiodism and Temperature.

Growth and dormancy in Norway spruce has been more widely studied than for Sitka spruce (Dormling et al. 1968, Robak & Magnesen 1970). Extension of daylength did not compensate for unfavourable temperatures in the growth of Norway spruce seedlings, and an abnormally short photoperiod reduced growth regardless of temperature (Magnesen 1969). Heide (1974a) found that temperatures between 12° and 24°C did not alter appreciably the critical daylength of various Norway spruce provenances, but higher temperatures accelerated the short day

response. Thus temperature may cause modifications in the process of growth termination, although not the causal factor itself.

Photoperiodic and temperature effects:

1) on bud formation.

The interaction of temperature and photoperiod has also been shown to influence bud formation. Burley (1966b) considered the onset of dormancy to be a response to adverse conditions at the seed source, while bud formation could be hastened by relatively high temperatures immediately after the critical daylength was reached. Sitka spruce seedlings grown in a greenhouse developed terminal buds more rapidly than those in a nursery, indicating the promotion of bud formation at high temperatures.

A similar result under warm conditions was obtained by Magnesen (1969) with Norway spruce, who showed that bud formation was mainly affected by temperature conditions during the last part of the growing season. Further experiments (Magnesen 1971) examining the influence of periods of low night temperature at different times of the season, resulted in early bud set when given relatively late in the season, but had no effect at all when photoperiods were comparatively long. Bud development is an active growth process favoured by high temperature, but these results show that plants can be stimulated to bud formation by low temperature, if the night length is long enough to have brought the

plants into a receptive stage.

2) on bud development.

The direct effects of temperature on needle initiation in Sitka spruce has not been studied, but provenance variation in needle initiation is well documented (Burley 1966a). Rapid development of primordia characterised northern Sitka spruce provenances (Pollard et al.1975), while southern provenances exhibited a slower rate of accumulation over a longer period. This was thought to be an adaptation to the period available for bud morphogenesis at the latitudes of origin and as the experiment was in a constant controlled environment, the pattern of morphogenesis was presumed to be under endogenous control. A field study (Cannell & Willett 1975) of the variation in needle initiation in Sitka spruce, growing in Scotland, agrees with the findings of Pollard et al. (1975) regarding duration, but rates of initiation were similar for all provenances. Southern provenances consequently predetermined up to 100 more needles than northern sources.

The importance of temperature conditions during bud development of black spruce (Picea mariana (Mill.) B.S.P.) and white spruce (Picea glauca (Moench) Voss) seedlings has been shown by Pollard & Logan (1977). Temperatures $\geqslant 25^{\circ}C$ proved optimal for needle initiation, and results indicated that temperature affects mainly the rate of initiation rather than its duration, in these species.

3) on subsequent growth.

The after effects of photoperiod and temperature treatments in the period following budset, on growth of Norway spruce in subsequent years has been investigated (Dormling et al. 1968, Skre 1972, Heide 1974b). The daylength and temperature during maturation of the terminal bud determines the amount of dormancy obtained, the time of bud break and the amount of growth made in the next flush (Dormling et al. 1968). Bud maturation at sub-optimal temperatures - too high or too low - was shown to cause a dormancy which requires a cold treatment for breakage, whereas buds matured in short days with optimal temperatures (20°C) will flush in long days (Dormling et al.1968). Similar results of deeper dormancy induced by high temperatures and consequent delayed flushing were found by Heide (1974b), who attributed this response to the effect of temperature on the differentiation of shoot and needle primordia.

5:2 Introduction.

To investigate the interaction of temperature and photoperiod on the setting and maturation of buds, an experiment was conducted in growth rooms. The effect of these treatments on flushing was followed in the spring.

The seedlings used were from the IUFRO collection of 1970. Similar seedlings were used in a nursery test in the same year by Kraus & Lines (1976), while Pollard et al. (1975) have also studied the influence of declining photoperiod on seedlings from this collection.

5:3 Materials and Methods.

Treatments

The four temperature treatments and associated conditions (Table 5:1) were selected to relate to those at the latitudes of origin (Schober 1962), and to the suggested optimal temperature for photosynthesis in Sitka spruce (Nielson et al. 1972). All temperature treatments received the same photoperiod, which was progressively reduced from 19h. at the start of the experiment, by hourly decrements each week to 17h. and then by 30 min. wk^{-1}. The 12.5h. critical daylength recorded by Lines & Mitchell (1966) for the cessation of growth of southern provenances of Sitka spruce, was used as a guideline when planning the treatments.

TABLE 5:1 Experimental treatments in controlled environment rooms.

Temperature °C		Relative Humidity %		Vapour pressure deficit (mb)	
Day	Night	Day	Night	Day	Night
20	11	91	96	2.0	0.5
16	9	89	96	2.0	0.5
12	7	86	95	2.0	0.5
8	5	82	82	1.9	1.9

The daily illumination cycle was as follows :-

e.g. a 16h day 2.5h tungsten (daylight) bulbs
11h bright, fluorescent light and tungsten bulbs
2.5h tungsten bulbs
8h darkness.

The light intensity during the bright period was 14,000 lux at plant level and decrements were made in this period. The soil was maintained at field capacity by daily watering and additions of liquid fertiliser made twice weekly.

Plant material.

One year old Sitka spruce seedlings selected from the IUFRO collection, spanning a latitudinal range of 17°N, and one and two-year old clonal cuttings, as detailed in Table 5:2, were potted in April 1973, and 'plunged' out of doors until midsummer.

TABLE 5:2. Plant Material.

Provenances of Sitka spruce (I.U.F.R.O. Collection).

I.U.F.R.O. No.	Provenance Location	Latitude N.	Longitude W.	Elevation (m)
3022	Dyea, Alaska.	59°50'	135°35'	0
3032	Kitwanga, Skeena/ Nass R.,B.C.	55°17'	127°87'	670
3050	Copper Creek, Moresby Is.	53°13'	131°80'	80
3059	Fair Harbour, Vancouver Is.	50°05'	127°03'	30
3064	Vedder, Chilliwack, B.C.	49°12'	121°93'	30
3002	Port Angeles, Washington.	48°15'	123°73'	110
3013	Tillamook, N. Oregon.	45°33'	123°88'	90-120
3017	Gold Beach, Oregon.	42°50'	124°42'	30

Sitka spruce clonal cuttings.

8000	Probable Q.C.I.	1 year old.
8014	" "	2 year old.

Experimental design.

At the time of maximum natural photoperiod (19.75h on 24 June 1973, in the Edinburgh area), the plants were allocated randomly to treatments and transferred to four growth rooms. In each growth room the provenance seedlings were arranged in 15 randomised blocks, each of eight plants. Each provenance had 15 seedlings per treatment, apart from the most southern provenance (3017) with only 12 seedlings per treatment. Ten plants of clone 8000 and five plants of clone 8014 were arranged in a single randomised block in each growth room.

Measurements.

Height measurements and recordings of the condition of the terminal apices were made weekly. As there was considerable variation in weekly height increment within provenances and in individual plants in successive weeks, it was desirable to have some objective criterion of growth cessation. Extension growth was considered to have ceased, when the difference between the sample means of successive measurements did not exceed 1.6mm, which was the detection limit of any change in height (detection limit = 3 x standard deviation of repeated measurement).

When extension growth had ceased in all provenances in all treatments, the plants were removed from the growth rooms and wintered outdoors. The effect of the treatments on the time of flushing in 1974 was followed in the open.

Statistical analysis.

The following variates, for both provenances and clones,

were subjected to an analysis of variance :- the height gain at cessation of growth, the height gain at the end of the experiment, the difference between these two heights, and the time of cessation of growth (or growth duration).

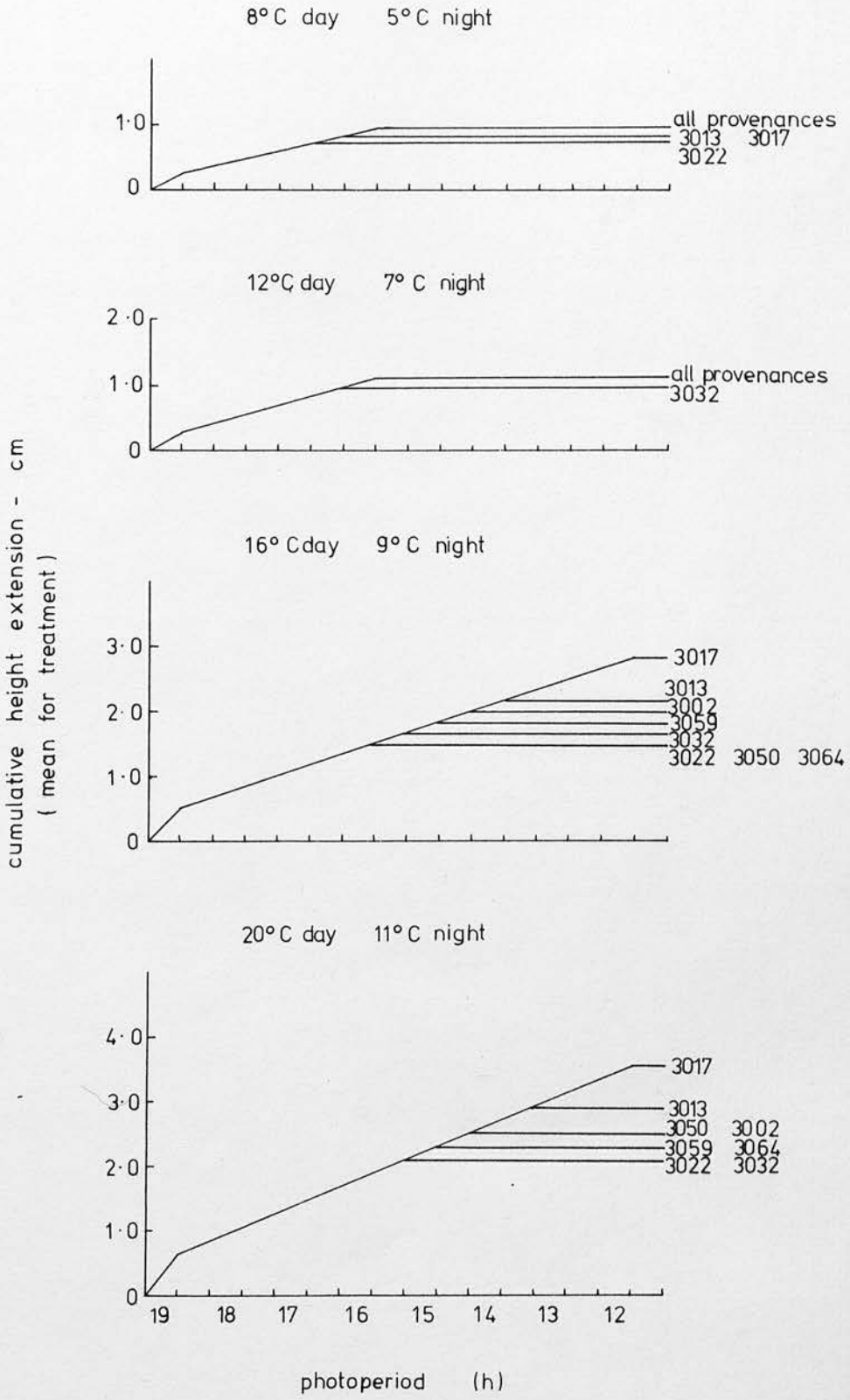
5:4 Results.

The effect of the temperature treatments on the cessation of shoot extension of the provenances under declining photoperiods and the differences in rate of cumulative height growth, are shown in Figure 5:1. The daylengths at which extension growth ceased in the different temperature regimes are given in Table 5:3, from which the order of cessation in the different plant types can be seen.

TABLE 5:3 Photoperiod at time of extension growth cessation (h).

Treatment	8/5°	12/7°	16/9°	20/11°
Provenance				
3022	17	16	16	15.5
3032	-	16.5	15.5	15.5
3050	16	16	16	14.5
3059	16	16	15	15
3064	16	16	16	15
3002	16	16	14.5	14.5
3013	16.5	16	14	13.5
3017	16.5	16	12	12
Clone				
8000	18	18	19	19
8014	18	18	18	19

FIGURE 5:1 The interaction of temperature and photoperiod on cessation of shoot extension of Sitka spruce provenances.

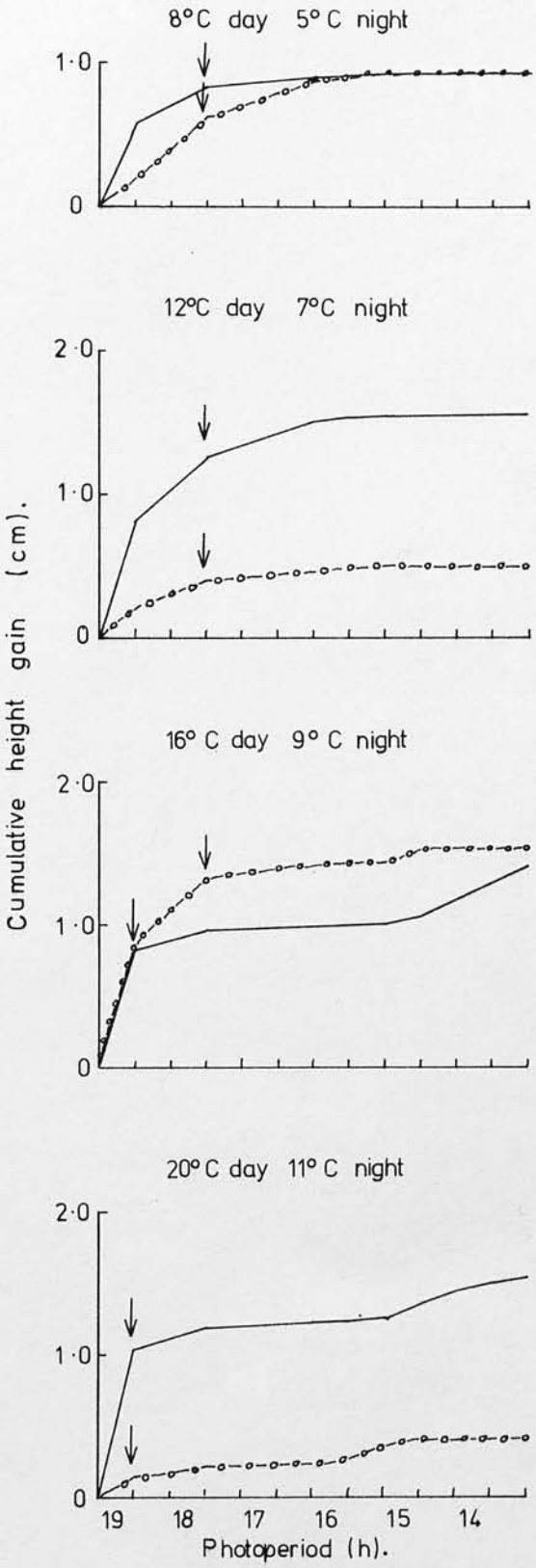


At the two cooler temperature regimes (8/5°C and 12/7°C), all provenances ceased height growth when the photoperiod reached 16h., whereas growth of southern provenances continued until the photoperiod was reduced to 12h. in the warmer regimes (16/9°C and 20/11°C).

Shoot extension in the two most northerly provenances ceased at a photoperiod of 15.5h. in all temperature treatments. In provenance 3032 a high proportion of the plants had already formed terminal buds prior to the treatments, by the longest photoperiod of 19.75h. and no extension growth was detectable at the coolest temperature regime. The southern provenances displayed a wider range of temperature effects, with the cooler regimes resulting in cessation of height growth at the relatively long daylength of 16.5h.

The interaction of temperature and photoperiod on growth cessation in the clonal cuttings is shown in Figure 5:2. At the coolest temperature the clones response was similar and growth ceased at a photoperiod of 18h. Only at 16/9°C did the photoperiod at growth cessation differ between the clones. Neither differences in height growth at the different temperature regimes or between clones were significant - see analysis of variance tables, Appendix 5. At the two warmer temperatures reflushing of some plants complicated the detection of growth cessation. Reflushing occurred in both clones at a photoperiod of 16.5h. at 20/11°C, ($\frac{6}{10}$ for 8000, $\frac{1}{5}$ for 8014) and at 16h. at 16/9°C ($\frac{6}{10}$ for 8000, $\frac{4}{5}$ for 8014). Unlike clone 8000, clone 8014

FIGURE 5:2 The interaction of temperature and photoperiod on cessation of shoot extension of clonal Sitka spruce. Arrows denote critical photoperiod. ———— 8000 —•—•—•—•—•— 8014



had a large proportion of plants already set bud by the start of the experimental treatments. Provenance 3032 which had also set terminal buds, was the only provenance which reflushed during the experiment: $\frac{8}{15}$ at 16/9°C and $\frac{5}{15}$ at 20/11°C.

Differences in rate of shoot extension were noted for each provenance in the four temperature treatments. This, coupled with the differences in time of growth cessation, accounts for the large variation in height attained between treatments. The 20/11°C treatment resulted in the greatest height increments, due to greater growth rates and particularly, longer periods of growth. (Table 5:4). Analysis of variance confirms the strong influence of temperature on provenance height growth, while showing significant ($p \leqslant 0.01$) inherent differences between provenances, following a clinal trend with latitude (Appendix 5).

TABLE 5:4 Mean height growth of provenances (cm), from data sheets.

Treatment	8/5°		12/7°		16/9°		20/11°	
Provenance	a	b	a	b	a	b	a	b
3022	0.6	0.9	1.2	1.6	1.8	1.9	2.4	2.5
3032	0.0	0.3	0.5	0.8	1.8	2.0	1.9	2.0
3050	1.3	1.5	1.2	1.7	1.7	2.4	2.7	2.8
3059	1.2	1.4	1.7	2.3	2.3	2.6	3.1	3.4
3064	1.1	1.4	1.2	1.9	1.6	2.2	2.6	2.8
3002	1.0	1.2	1.4	1.9	2.5	2.7	3.2	3.3
3013	0.7	1.2	1.5	2.2	2.4	2.6	3.7	3.9
3017	0.8	1.2	1.4	2.3	3.0	3.0	4.8	4.8
Clone								
8000	0.8	0.9	1.2	1.5	0.8	1.4	1.0	1.5
8014	0.6	0.9	0.4	0.5	1.3	1.5	0.1	0.4

a) when weekly extension no longer detectable.
b) at end of experiment.

Although the limit of detection of height increment provided a useful criterion of growth cessation for each plant sample, many plants continued to make additional extensions during the remainder of the experiment. These additional increments are shown in Table 5:4.

To take the variation in successive height increments of individual plants into account, an analysis of variance was performed in which the cessation of growth for each plant was assumed to occur when its weekly increment first fell below 1.6mm.:-

Source of Variation	DF	SS	MS	VR	F 5%	F 1%
Provenance	7	102.3	14.6	5.0	2.03	2.69
Temperature	3	685.4	228.5	79.0	2.62	3.83
Interaction	20	484.9	24.2	8.4	1.60	1.92
Residual	387	1119.1	2.9			
Total	417	2391.8				
Clones	1	13.6	13.6	15.0	4.08	7.29
Temperature	3	15.2	5.1	5.6	2.84	4.30
Interaction	3	2.5	0.8	0.9	(2.84)	(4.30)
Residual	41	37.2	0.9			
Total	48	68.5				

For the provenances, all the variance ratios are highly significant ($p \leqslant 0.01$), but the overriding influence of the temperature treatments on the time of growth cessation is clear. For the clones, only the clonal and temperature variance ratios are significant ($p \leqslant 0.01$) and the clonal effect dominates the influence of temperature.

The mean duration of growth in weeks after the

summer solstice, based on individual plants from the analysis of variance, is given by plant group and temperature treatment in Table 5:5. The provenances show a latitudinal trend in termination of extension growth, comparable with the field results of Lines & Mitchell (1966), while the duration of growth doubles between the coolest and warmest treatments. No obvious trends are shown by the clones, although both have their longest growth period at the lowest temperature, in contrast to the provenances. The results in Table 5:5 however, do not take into account the height growth made in the second flush by the clones.

TABLE 5:5 Mean duration of height growth (weeks) for individual plants, taken from analysis of variance.

Treatment / Provenance	8/5	12/7	16/9	20/11°	Overall Mean
3022	3.38	5.50	4.86	5.83	4.89
3032	3.02	4.39	5.61	5.18	4.55
3050	5.00	5.20	6.07	6.20	5.62
3059	4.67	5.20	6.53	6.40	5.02
3064	4.13	4.14	5.27	6.53	5.70
3002	4.20	5.46	5.67	7.60	5.73
3013	3.54	4.79	5.73	8.47	5.63
3017	2.51	4.67	4.58	12.25	6.00
Overall Mean	3.84	4.93	5.56	7.18	
Clone					
8000	2.50	2.33	1.44	1.40	1.9
8014	3.99	2.67	2.40	2.67	2.9
Clonal Mean	3.24	2.50	1.92	2.03	

Bud development was enhanced by the higher temperatures; terminal buds becoming visible 1-3 weeks after height growth ceased in the 20/11°C treatment and 2-6 weeks later in the 16/19°C treatment. In the two cooler treatments buds could only be detected visually 8-9 weeks after cessation of growth. Differences between provenances in the timing of bud development were not large and although no analysis of these observations was made, the differences are not thought to be significant.

The influence of the different temperature regimes during bud maturation on flushing in the spring of 1974 was recorded in the open. The first assessment was made on 22 April 1974, by which time certain plant groups had already flushed. The date of flushing (50% per group) is expressed as the number of days after the first day of the year which had a mid temperature $\geqslant 5^{\circ}C$ (Table 5:6), taken from minimum and maximum temperatures (Appendix 5). The date of flushing is also related to the number of days after growth cessation, that the plants remained in the growth rooms i.e. the length of bud maturation under the experimental treatments (Table 5:6).

Breaking of bud dormancy followed a latitudinal trend from northern to southern provenances, with northern provenances flushing in response to cooler spring temperatures. Southern provenances flushed up to one month later and displayed greater variation between treatments. Plants formerly at 8/5°C - the coolest and longest bud maturation period - tended to flush first, with little

variation in the mean time to flushing at the other temperature regimes. The high elevation provenance 3032, flushed consistently early. The clones flushed later than the provenances and their response does not fit the latitudinal trend or the trend related to pre-treatment.

TABLE 5:6 Flushing in Spring 1974.

Treatment	8/5		12/7		16/9		20/11		Overall Mean.	
Provenance	a	b	a	b	a	b	a	b	a	b
3022	91	46	77	56	77	59	70	46	79	52
3032	112	46	84	46	70	46	70	46	84	46
3050	77	46	77	63	77	63	56	46	72	55
3059	77	46	77	59	63	59	63	63	70	57
3064	77	46	77	59	77	66	63	70	74	60
3002	77	46	77	66	56	66	56	70	67	62
3013	84	59	77	73	49	70	42	73	63	69
3017	84	49	77	63	21	59	21	70	51	60
Overall Mean	85	48	78	61	61	61	55	61		
Clone										
8000	98	66	98	66	105	73	105	77	102	71
8014	98	73	98	77	98	73	105	70	100	73
Clonal Mean	98	69	98	71	101	73	105	73		

a) number of days bud maturation at treatment temperatures after growth cessation,

b) number of days after mid-temperature $\geqslant 5^{o}C$ i.e. 4 March 1974.

5:5 Discussion

Bud formation in Norway spruce tends to occur slightly earlier in nursery than in glasshouse grown plants and Dormling (1973) attributes this to a temperature effect

once a critical night length has made the plants receptive to lower temperatures. In the experiment reported here, although the temperature regimes were constant and did not include night temperatures below 5°C, they had marked effects on the photoperiod at which apical shoot growth ceased. As the experiment began at midsummer, it is unlikely that any photoperiodic conditioning could have taken place, yet the lower temperature regimes resulted in no further shoot extension after the photoperiod had reached 16h. The same provenances growing in the field, where environmental stresses may be greater, had a much shorter critical daylength (Kraus & Lines 1976). Comparable first year seedlings grown at constant 22.5°C under declining photoperiod (Pollard et al. 1975), ceased growth at photoperiods in line with the results of Kraus & Lines (1976). It would seem that the low temperatures in this experiment are the clue to growth cessation at longer daylengths. In the field, temperatures would not reach 8°/5°C or 12°/7°C until much shorter daylengths. Differing criteria for growth cessation and the frequency of measurements, could also be involved in these conflicting results. The large number of provenances studied by Kraus & Lines, necessitated less frequent growth measurements than was possible in this experiment.

Provenance 3032 from an area of introgression with white spruce (P. glauca (Moench) Voss), may be an exception with regard to photoperiodic preconditioning prior to the experiment, since a number of these plants had already set

terminal buds. Such a response indicates an adaptation to a short, warm season, also signified from results in the nursery, where this provenance stopped growing two weeks earlier and set terminal buds one week earlier, than other sources of comparable latitude (Kraus & Lines 1976). A similar instance for a Norway spruce provenance from latitude 64°N is discussed by Heide (1974a).

The plants used in this experiment were lifted from the same bed of a nursery provenance trial and potted before flushing in their second year. They thus had buds which would be extended into shoots of a predetermined length after flushing in early May and the experiment was designed to start before extension growth would normally be expected to cease. Growth continuing beyond that predetermined in the bud, has been termed 'free' and shown to occur in the early years of several species and has been demonstrated for four-year old black spruce provenances in Canada (Pollard & Logan 1974). These authors further demonstrated (1975) that 'free' growth could be induced in the second growth cycle of black spruce by a high temperature treatment (25°C) at photoperiods in excess of 12h. It seems probable that the Sitka spruce provenances in this experiment, at the higher temperatures, were in 'free' growth.

This is supported by the comparison of duration of growth between these two-year seedlings and the two vegetatively propogated clones of older Sitka spruce.

Neither clone, of probable Queen Charlotte Islands provenance, grew for more than three to four weeks in any treatment indicating that they had little or no capacity for free growth in these conditions. The effect of age on the sensitivity of white spruce seedlings to the dormancy - inducing influence of short days has been shown by Pollard (1973); increasing age causes seedlings to be increasingly susceptible to treatment. The tendency in the clones to reflush at the two warmer temperatures, at daylengths of 16.5h. and 16h, indicates an interaction with temperature so reducing the critical daylength.

From Table 5:3 it appears that the highest temperature had the greatest effect on duration of growth and that it was related inversely to latitude of origin. Conversely the southern provenances seem to be more sensitive to low temperatures (Table 5:5) than those origins from the middle of the range. These results support Pollard & Logan's contention that 'free' growth is environmentally controlled.

From the literature and the results of this experiment it appears that temperature influences growth cessation and bud formation - cool temperatures hastening growth cessation and warm temperatures hastening bud formation.

Differences in observable bud formation between provenances have been reported by Kraus & Lines (1976), who found southern origins to be more rapid than northern origins. Pollard et al. (1975) however, from primordial counts, found the opposite to be true. In this study,

differences in timing of the appearance of terminal buds between provenances were small and did not follow a latitudinal trend. It is not yet clear whether bud development is entirely endogenously controlled or the extent to which it is influenced by environmental factors.

Flushing in the spring followed the general pattern described by Burley (1966b), of northern provenances first with greater variation in the southern provenances. Provenance 3032, an inland source flushed early from all treatments. This response is in agreement with the findings of Burley (1966b) for inland provenances, where once the minimum temperature for growth occurs, the chance of frost is very slight and flushing starts. However, both Burley and Roche (1969) found a negative correlation between flushing and altitude, therefore the early flushing of the high altitude 3032 may result from possible introgression with white spruce. Low temperature treatments during bud maturation appeared to advance flushing dates in all provenances, in comparison to the warmer treatments, in line with the view that warmer temperatures induce a deeper dormancy (Dormling et al. 1968).

5:6 Conclusion.

In general the results show that photoperiod does not control cessation of apical shoot extension in Sitka spruce absolutely, but that higher temperatures may be important in shortening the critical daylength, while low temperatures appear to upset the commonly accepted

latitudinal relationship between photoperiod and growth cessation. The effect is marked among the southern provenances which appear to be more plastic in their temperature response than those from the north. For example, the Oregon provenances (3013, 3017) varied by more than 3h. in the length of their critical photoperiod, compared to only 0.5h. for the sea-level Alaskan provenance (3022).

Bud development to the stage where it becomes visible is clearly affected by the ruling temperature regime. At low temperatures the process of development is slower.

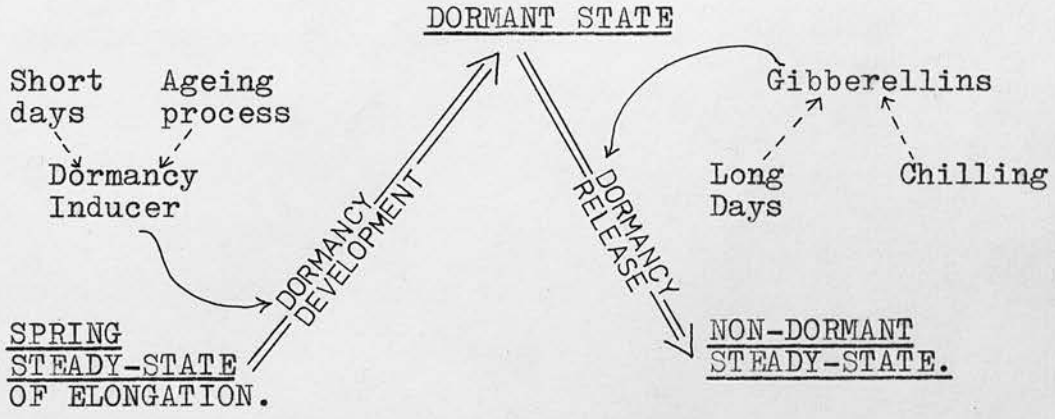
Temperature conditions during bud maturation appear to affect the time of flushing the following year. Plants from the coolest temperature regime (8/5°C) flushed first. A tendency towards a clinal trend in flushing with decreasing latitude was observed.

CHAPTER 6. TO DEFINE THE MINIMUM CHILLING REQUIREMENTS OF SITKA SPRUCE.

6:1. Literature review.

Dormancy has been defined as "any case in which a tissue predisposed to elongate does not do so" (Doorenbos 1953). However, dormancy is not a simple inhibition of elongation growth as the reviews on this subject point out (Doorenbos 1953, Samish 1954, Wareing 1956, Romberger 1963) and it is unlikely that one comprehensive theory can be established to explain dormancy.

Smith and Kefford (1964) suggest dormancy to be a succession of processes and that three steady-state and three transitional phases follow each other, in the development of dormancy, thus :-



In contrast to the separate phases in dormancy proposed by Smith and Kefford, Lavender and Hermann (1970) suggest physiological changes during the dormant period to be correlated with changes in the relative concentrations of growth inhibitors and promoters.

Under natural circumstances, winter dormancy is

broken in north temperate coniferous species by exposure to chilling (Dormling et al. 1968, Neinstaedt 1966, 1967, Worrall and Mergen 1967). A sufficiently long period of cold causes buds to pass from winter dormancy to imposed dormancy and bud break occurs when temperature conditions are favourable (Worrall and Mergen 1967). High temperatures interrupting the chilling period, during the early phases of dormancy release, may counteract any previous low temperature treatments (van den Driessche 1975).

Picea species have been shown to require a winter chilling treatment to produce uniform flushing and normal shoot growth (Neinstaedt 1966, 1967, Dormling et al. 1968). Insufficient chilling of Sitka spruce seedlings led to irregular growth and abnormal terminal shoots (Herbert 1971). The percentage of abnormal plants decreased markedly with the intensity or duration of winter chilling.

Neinstaedt (1966) working with two year-old white spruce seedlings, found a chilling period of 4-8 weeks at 2° to 4°C released dormancy, though the chilling requirement varied with the age of the plant and with the timing of the treatment. Young plants required more chilling than older ones and plants exposed to chilling in July required more chilling than plants treated in September. Further experiments with seven Picea species (Nienstaedt 1967) showed all species to require some chilling (6-8 weeks at 4°C) for prompt dormancy break

and that long days after chilling compensated for insufficient chilling periods. Within species variation indicated that northern sources may require more chilling than southern sources.

The requirement of a chilling period in the normal growth cycle of Picea species is accepted, however for P. abies seedlings a cold treatment was found to be unnecessary to break dormancy, if buds had been matured long enough in short-day conditions at 20°C (Dormling et al. 1968). Long days alone sufficed and shoot extension did not vary significantly from plants previously chilled. Differences were found in the appearance of the plants - chilled plants developed shoots with longer, slender needles. These results show how environmental conditions during bud maturation affect the depth of dormancy, the conditions necessary to break dormancy and the subsequent amount of growth made.

The interacting effects of chilling, photoperiod and flushing temperature on growth of Douglas fir seedlings (Pseudotsuga menziesii (Mirb.) Franco) have been studied by Campbell and Sugano (1975). Effects induced by chilling depended on the timing, duration and chilling temperature. After induction by a single chilling temperature and period, rates of bud burst were also influenced by photoregime and temperature during flushing. The influence of flushing temperature on the expression of the induced effects of chilling, depended on the duration of chilling. The concept

of potential and realised DARDS (percentage daily average rate of development, towards bud burst) is presented; potential DARDS are an induced response, that depend on duration and temperature of pre-chilling and chilling, while realised DARDS are a function of this potential, plus photoperiod and temperature during the time of realisation. Bud burst is achieved when realised DARDS sum to 100. The responses to environmental treatments were quantitative and continuous and Campbell and Sugano suggest that the dormancy phases in Douglas fir do not follow the separate growth - regulator patterns as proposed by Smith and Kefford (1964), but rather the concept put forward by Lavender and Hermann (1970).

Van den Driessche (1975) in his study on Douglas fir, also found increased chilling led to more rapid flushing at lower daily average temperature. This result agrees with the generally accepted view that as the breaking of dormancy becomes more complete, due to continued chilling, growth becomes possible over a wider range of temperature conditions.

6: 2. Introduction.

The chilling requirements of Sitka spruce have not been studied in detail. To complete the study of temperature effects on the vegetative growth cycle, a chilling experiment was designed to determine the minimum chilling requirements of a range of provenance seedlings.

6: 3. Materials and Methods.

Treatments.

Three chilling treatments of 0°, 3° and 6°C were

chosen with five chilling periods of 1, 2, 4, 6 and 8 weeks.

The growth rooms used in the earlier experiments only function down to 4°C, so alternative facilities had to be found for the two cooler temperatures. A cold room at the Forestry Commission Northern Research Station was used for the 3°C treatment and proved very reliable with little temperature variation. A growth room at King's Buildings, University of Edinburgh, was used for the 0°C treatment and this temperature proved the most difficult to maintain. The temperature did rise to 1°C on occasions but rarely reached 2°C.

All chilling treatments received the same photoperiods of 8h. and a light intensity of 2,000 lux provided by fluorescent tubes and tungsten filament bulbs.

Plants subjected to no chilling treatment acted as controls in a heated greenhouse, with an 18h. photoperiod.

At the end of the chilling period plants were removed to a heated greenhouse with an 18h. photoperiod. Temperature in the greenhouse was 15°C minimum and 20°C maximum until 6.12.73. The oil crisis in the winter of 1973 unfortunately necessitated a drop in temperature in early December to 10°/13°C, but records of minimum/maximum temperatures show that in fact minimum temperatures were as low as 8°C during December 1973 and January 1974, and averaged 11°C from February to April 1974. In Chapter 3 the delaying effects of low temperature on flushing were demonstrated and this change in the experimental temperature half-way through, to some extent nullifies some of the results.

Plant Material.

One year old Sitka spruce seedlings selected from the I.U.F.R.O. collection and two year old cuttings of clone 8000, detailed in table 6:1, were potted in April 1973 and 'plunged' out of doors for the growing season.

Table 6:1. Plant Material.

Provenances of Sitka spruce (I.U.F.R.O Collection).

I.U.F.R.O. No.	Provenance Location.	Latitude N.	Latitude W.	Elevation m.
3028	Old Hollis, Alaska.	55°47'	132°67'	0
3032	Kitwanga, Skeena/ Nass R., B.C.	55°17'	127°87'	670
3053	Jedway, Moresby Is.	52°28'	131°22'	15
3059	Fair Harbour, Vancouver Is.	50°05'	127°03'	30
3064	Vedder, Chilliwack, B.C.	49°12'	121°93'	30
3004	Kalaloch, Washington.	47°70'	124°42'	0-30
3011	Astoria, N. Oregon.	46°20'	123°97'	0-15
	Sitka spruce clonal cutting.			
8000	Probable Q.C.I., B.C.			

In May 1973 some of the provenance seedlings appeared to be frost-damaged and were replaced with seedlings from the nursery. In mid-October, the risk of night frosts made it necessary to move all the plants from the plunge beds to a heated greenhouse, until the start of the experimental treatments.

Ten seedlings per provenance (except 3004 - 5 seedlings), and 10 clones were allocated randomly to each chilling period at each temperature on 26 October 1973, making a total of 75 plants per treatment.

Measurements.

The height of each plant was measured before placing in the treatment rooms. The time of terminal bud and subterminal flushing was measured in the greenhouse, as described in Chapter 3. The experiment was terminated in early June when shoot extension and the length of a branch of the current season whorl was measured.

Analysis.

The flushing data was subjected to an analysis of variance, both for individual provenances and the clone and for the experiment as a whole. Similarly, height gain and branch length were analysed by analysis of variance.

The correlation coefficients between height gain and branch length were computed.

6:4. Results.

Tables 6:2 and 6:3 show the number of days to the start of terminal and subterminal flushing and the duration of flushing. Time to the start of flushing generally decreased with increasing periods of chilling in all temperature treatments. In all but two provenances (3053 and 3004), even the shortest chilling treatments had some beneficial effect on the start of flushing. The longer treatments however, resulted in more uniform flushing within a provenance X temperature treatment.

TABLE 6:2a. Number of days to the start of terminal flushing.

		Chilling period (weeks)					
	Temp	0	1	2	4	6	8
3028	None	133					
	0		132	114	96	87	84
(5.45)	3		114	120	95	73	62
	6		129	120	92	75	62
3032	None	115					
	0		108	94	72	67	43
(4.51)	3		98	87	70	60	52
	6		105	95	72	55	43
3053	None	124					
	0		126	119	91	71	51
(7.44)	3		129	113	84	72	55
	6		97	105	93	68	70
3059	None	141					
	0		122	117	92	67	57
(7.62)	3		105	116	103	73	61
	6		116	112	84	73	56
3064	None	134					
	0		116	96	93	83	60
(6.44)	3		111	106	85	72	70
	6		107	116	82	73	50
3004	None	122					
	0		123	106	95	75	56
ns	3		112	118	85	74	55
	6		123	112	81	73	-
3011	None	126					
	0		133	121	89	64	54
(7.94)	3		114	93	94	72	58
	6		107	98	79	59	53
8000	None	122					
	0		105	95	83	64	53
(5.12)	3		93	85	83	69	59
	6		109	106	78	67	50

Figures in brackets are values of D from Tukey's test.

TABLE 6:2b. Duration of terminal flushing in days.

			Chilling period (weeks)				
	Temp	0	1	2	4	6	8
3028	None	27					
	0		14	21	19	19	17
ns	3		22	19	23	23	22
	6		17	22	23	19	18
3032	None	20					
	0		20	21	18	23	18
ns	3		22	16	20	17	14
	6		21	22	19	17	15
3053	None	32					
	0		26	19	19	18	17
(4.40)	3		21	19	17	15	18
	6		33	35	18	18	16
3059	None	27					
	0		25	16	19	17	18
(3.96)	3		32	25	20	20	16
	6		20	23	19	16	18
3064	None	24					
	0		22	22	23	16	16
ns	3		21	20	15	16	15
	6		23	32	18	12	20
3004	None	36					
	0		39	20	19	16	18
(3.97)	3		19	26	18	15	15
	6		23	20	18	15	-
3011	None	37					
	0		24	24	18	17	18
ns	3		27	18	21	16	19
	6		41	33	24	19	17
8000	None	36					
	0		29	24	22	21	17
(3.32)	3		26	21	18	20	25
	6		26	27	21	16	18

Figures in brackets are values of D from Tukey's test.

TABLE 6:3a. Number of days to the start of subterminal flushing.

			Chilling period (weeks)				
	Temp	0	1	2	4	6	8
3028	None	111					
	0		105	101	80	69	64
(3.83)	3		101	105	86	64	57
	6		108	102	83	67	50
3032	None	113					
	0		105	89	70	65	40
(3.28)	3		100	83	68	57	46
	6		103	93	69	50	39
3053	None	88					
	0		93	89	76	55	41
(5.49)	3		94	87	71	58	45
	6		74	88	74	57	48
3059	None	102					
	0		85	89	77	52	44
(5.14)	3		71	90	83	62	53
	6		93	80	79	60	40
3064	None	99					
	0		89	79	78	62	43
(5.33)	3		89	78	74	58	48
	6		79	84	68	59	41
3004	None	79					
	0		94	77	70	60	45
ns	3		81	89	70	54	45
	6		82	86	69	57	-
3011	None	95					
	0		92	82	68	52	40
ns	3		87	74	68	56	48
	6		87	71	65	54	43
8000	None	108					
	0		85	81	72	60	41
(4.85)	3		72	71	69	61	55
	6		79	83	68	58	42

Figures in brackets are values of D from Tukey's test.

TABLE 6:3b. Duration of subterminal flushing in days.

			Chilling period (weeks)				
	Temp	0	1	2	4	6	8
3028	None	44					
	0		36	27	26	26	25
(3.77)	3		29	23	24	23	22
	6		30	34	22	21	18
3032	None	21					
	0		23	23	17	25	21
ns	3		21	20	19	20	19
	6		24	25	22	17	17
3053	None	28					
	0		35	31	26	24	18
ns	3		26	26	25	25	22
	6		25	33	30	22	25
3059	None	37					
	0		39	39	22	26	24
(4.78)	3		27	24	31	26	20
	6		27	29	19	24	24
3064	None	39					
	0		27	33	27	26	21
ns	3		36	25	20	25	31
	6		33	30	21	24	20
3004	None	25					
	0		50	27	32	25	22
ns	3		32	32	24	25	20
	6		39	33	21	23	-
3011	None	41					
	0		46	46	29	18	24
ns	3		39	20	27	24	24
	6		34	39	26	18	21
8000	None	36					
	0		24	23	27	18	20
(4.46)	3		22	13	27	24	24
	6		33	25	21	21	22

Figures in brackets are values of D from Tukey's test.

Subterminals started to flush before terminal buds in all provenance x treatments (excepting 3032 at 1 week 3°C) and in all control plants. From the analysis of variance tables (Appendix 6) it can be seen that the length of the chilling period was highly significant in determining when flushing started, accounting for 61% of the variation in terminal flushing of the provenances and 64% of the subterminal flushing. Any significant differences in the analysis of variance due to temperature are due to the control treatment, the three temperature treatments being indistinguishable.

Duration or rate of flushing appears to be less affected by chilling than the start of flushing, especially in the more northerly provenances - 3028, 3032 and 3053. The control plants not only began to flush later than the chilled plants, but their rate of flushing was also slower.

Using the criterion that chilling requirements are met when an additional day's chilling does not result in a day's acceleration of flushing (Worrall and Mergen 1967), a table of the "optimal" chilling treatments can be drawn up (Table 6:4). Whether further chilling than the treatments given would have enhanced flushing cannot be said.

The longest chilling period appears optimal for the start of flushing as indicated in the analysis of variance results (Appendix 6). No trends in temperature effects can be seen. Since chilling seems to have little effect on

duration of flushing and taking terminal flushing to be more important than subterminal flushing in regard to subsequent height growth, the optimal treatments for the start of terminal bud flushing, may be said to be the minimal requirement of these seedlings for the breaking of dormancy.

Table 6:4. Minimum chilling requirements (weeks) for terminal and subterminal flushing.

	START SUBTERMINAL	DURATION SUBTERMINAL	START TERMINAL	DURATION TERMINAL
3028	8×6^{o}	8×6^{o}	$8 \times \frac{3^{o}}{6^{o}}$	1×0^{o}
3032	8×6^{o}	4×0^{o}	$8 \times \frac{0^{o}}{6^{o}}$	8×3^{o}
3053	8×0^{o}	8×0^{o}	8×0^{o}	6×3^{o}
3059	8×6^{o}	4×6^{o}	8×6^{o}	2×0^{o}
3064	8×6^{o}	4×3^{o}	8×6^{o}	6×6^{o}
3004	$8 \times \frac{0^{o}}{3^{o}}$	8×3^{o}	8×3^{o}	$6 \times \frac{3^{o}}{6^{o}}$
3011	8×0^{o}	$6 \times \frac{0^{o}}{6^{o}}$	8×6^{o}	6×3^{o}
8000	8×0^{o}	2×3^{o}	8×6^{o}	6×6^{o}

Analysis of variance of the experiment as a whole shows that the provenances account for very little (5%) of the variation. The results do not show any differences in provenance requirement. The comparatively fast flushing of provenance 3032 (Tables 6:2 and 6:3), agrees with earlier results for this provenance - Chapter 5.

The drop in temperature in the greenhouse where the plants were placed after chilling, undoubtedly affected the flushing rates of the plants and this factor should not be overlooked when considering the results. Plants receiving 1, 2 and 4 weeks chilling, received 5, 4 and 2 weeks of

warmer flushing temperatures respectively before the drop in temperature, whereas plants from the 6 and 8 weeks chilling treatments went directly into the cooler greenhouse.

In contrast to the flushing results, variation in height gain in the experiment as a whole, appears to be mainly the result of provenance variation, consequently temperature and length of chilling period in the analysis of variance of individual provenances are of little significance. Height growth was very variable within a provenance and in some cases plants exposed to chilling made less extension growth than the control plants.

That the greatest shoot extension should coincide with the optimal chilling treatment in some provenances, may well be a chance effect, even though the earlier flushing could create a height differential if the plants made 'free' growth. Several provenances from the 8 week x 6°C treatment showed greatest shoot extension, which is surprising since a considerable number of plants were lost in this treatment. Some of the results from the analysis of variance for height growth (Appendix 6), in Figures 6:1 and 6:2 are based on estimated values.

Although the daylength (18h.) and temperature conditions in the greenhouse, and the soil water status were not limiting, some plants had set bud by the end of the experiment in early June. From visual observations bud set followed a clinal trend with latitude; all buds set in provenances 3028, 3032 and 3053, the majority of buds set in provenances 3059 and 3064 and about 50% bud set in

FIGURE 6:1 Height growth of Sitka spruce provenances after chilling treatments.

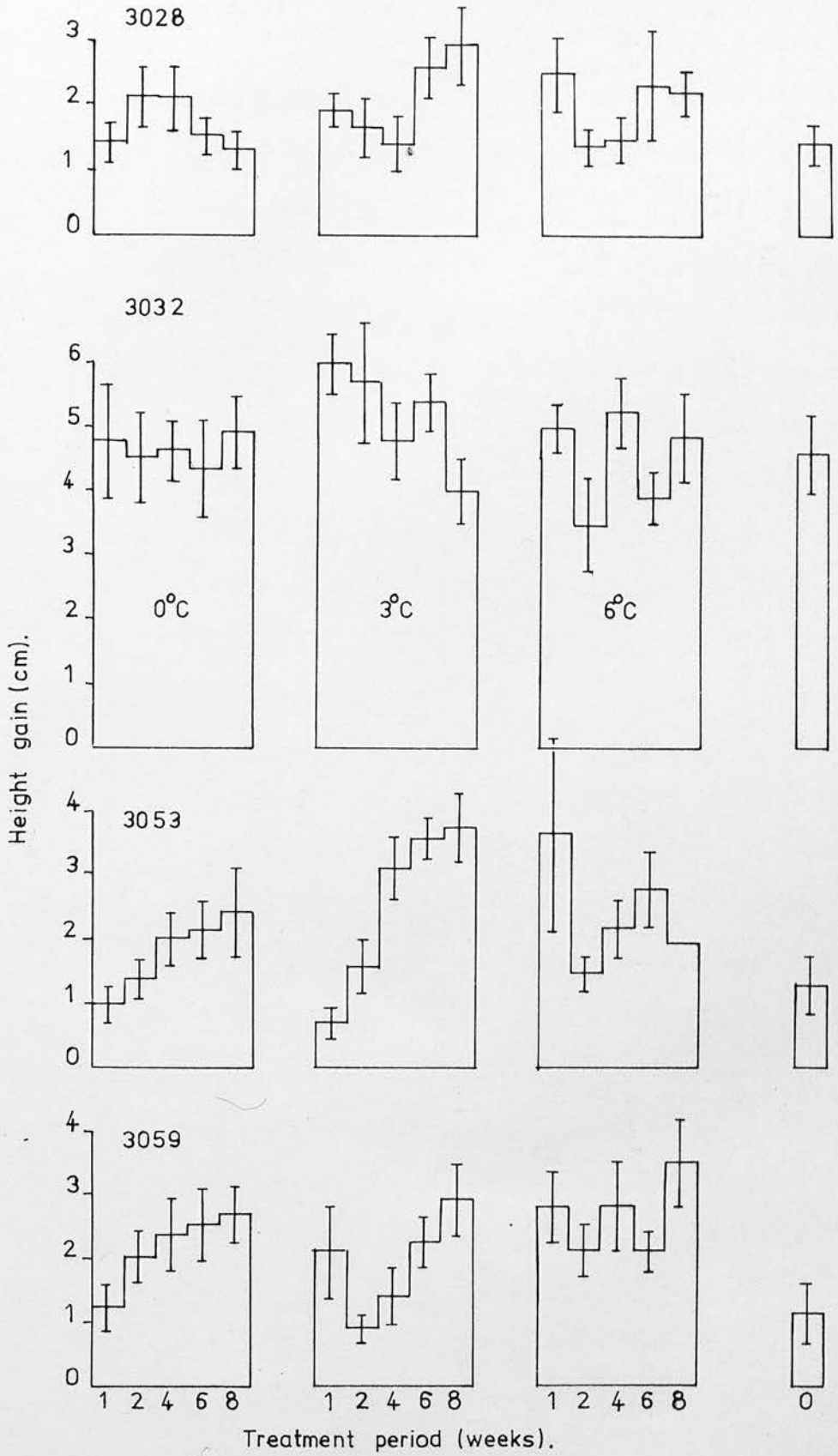


FIGURE 6:1 continued

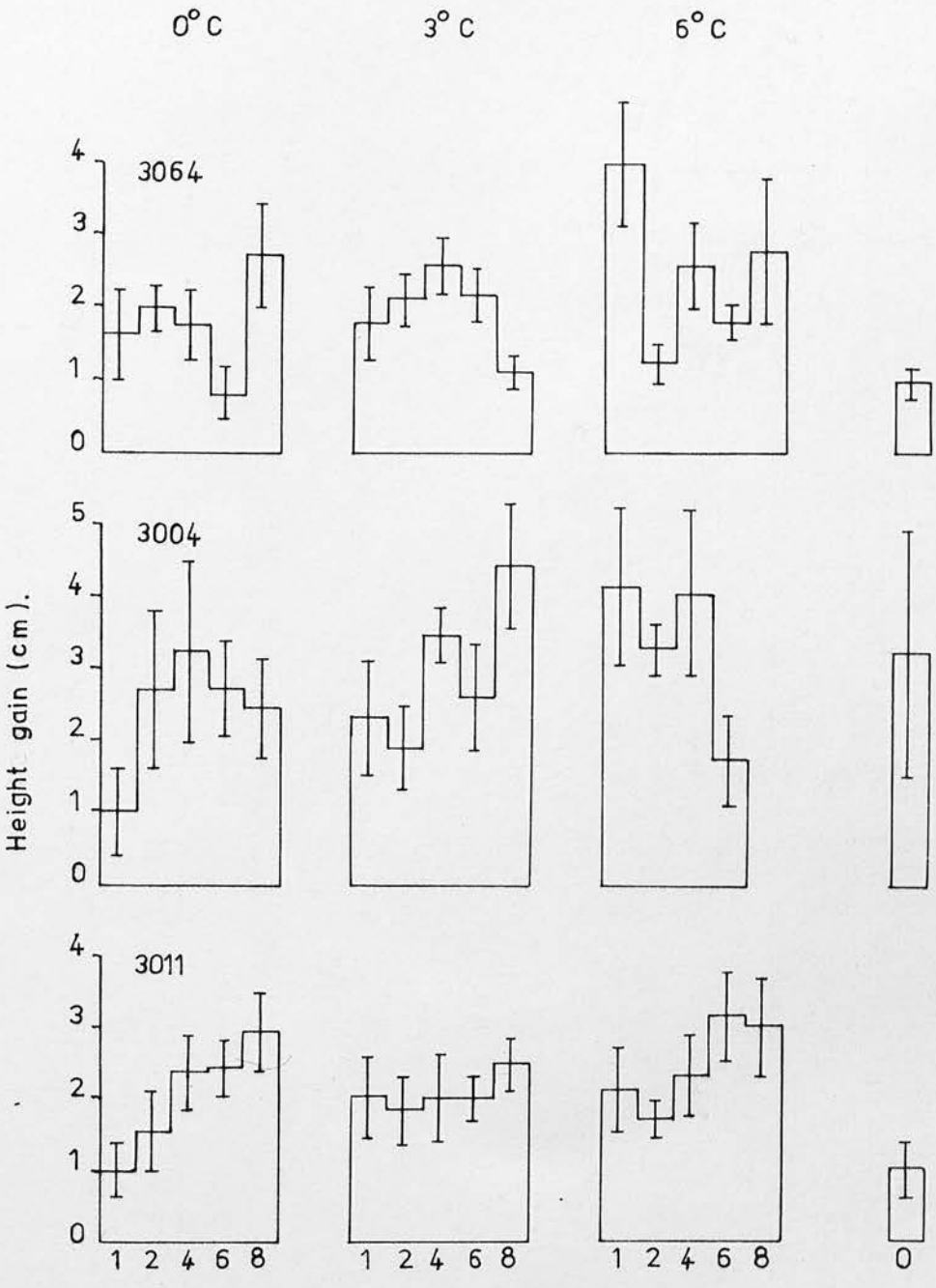
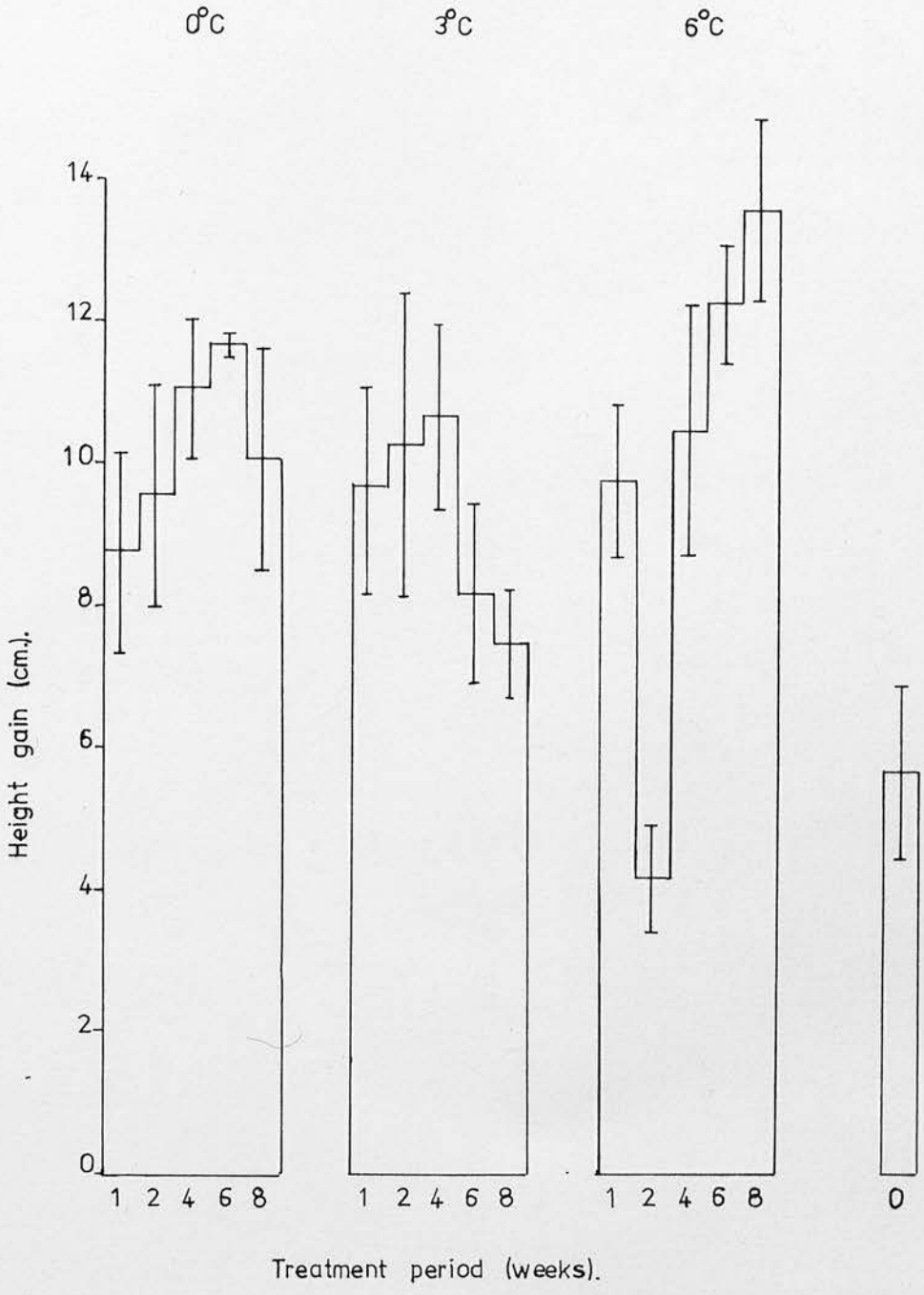


FIGURE 6:2 Height growth of Sitka spruce clone 8000 after chilling treatments.



provenances 3004 and 3011. Clone 8000 had all buds set. Control plants followed the same trend in respect to bud set.

Values of branch lengths measured at the end of the experiment are plotted in Figures 6:3 and 6:4. Again the variation seen is mainly due to provenance differences (see Analysis of Variance for whole experiment, Appendix 6). Comparing plots of height growth and branch length for each provenance, it can be seen that the histograms are of similar shape, with branch length generally exceeding leader extension.

The correlation coefficients of height gain and branch length show a high positive correlation. (Table A6:1, Appendix 6). There appears to be a trend of decreasing correlation with decreasing latitude, but results for provenance 3004 are slightly dubious due to the small number of replicates.

6:5. Discussion.

The chilling requirements of Picea seedlings have been shown to be satisfied by 4 to 8 weeks at $4^{\circ}C$ or less (Nienstaedt 1966). The results of this experiment for Sitka spruce are in line with the findings of Nienstaedt. For a range of provenances, the longest chilling period of 8 weeks, resulted in the most rapid and uniform start to terminal bud flushing, though the optimal chilling temperature varied with provenance. Samish (1954) points out that below a certain threshold temperature the effectiveness of chilling is not a function of temperature and all temperatures below the threshold value are equally

FIGURE 6:3 Branch lengths of Sitka spruce provenances after chilling treatments.

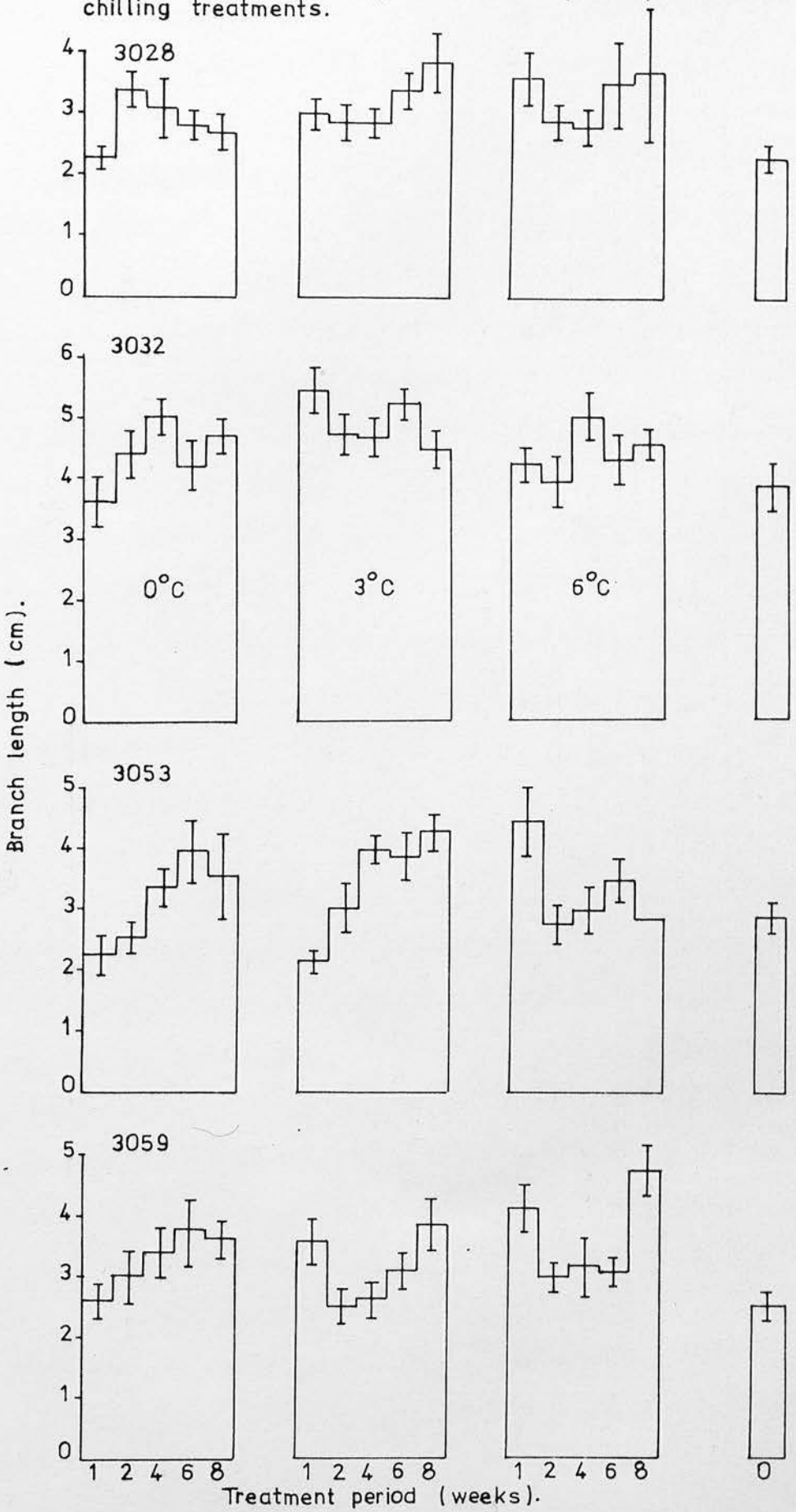


FIGURE 6:3 continued

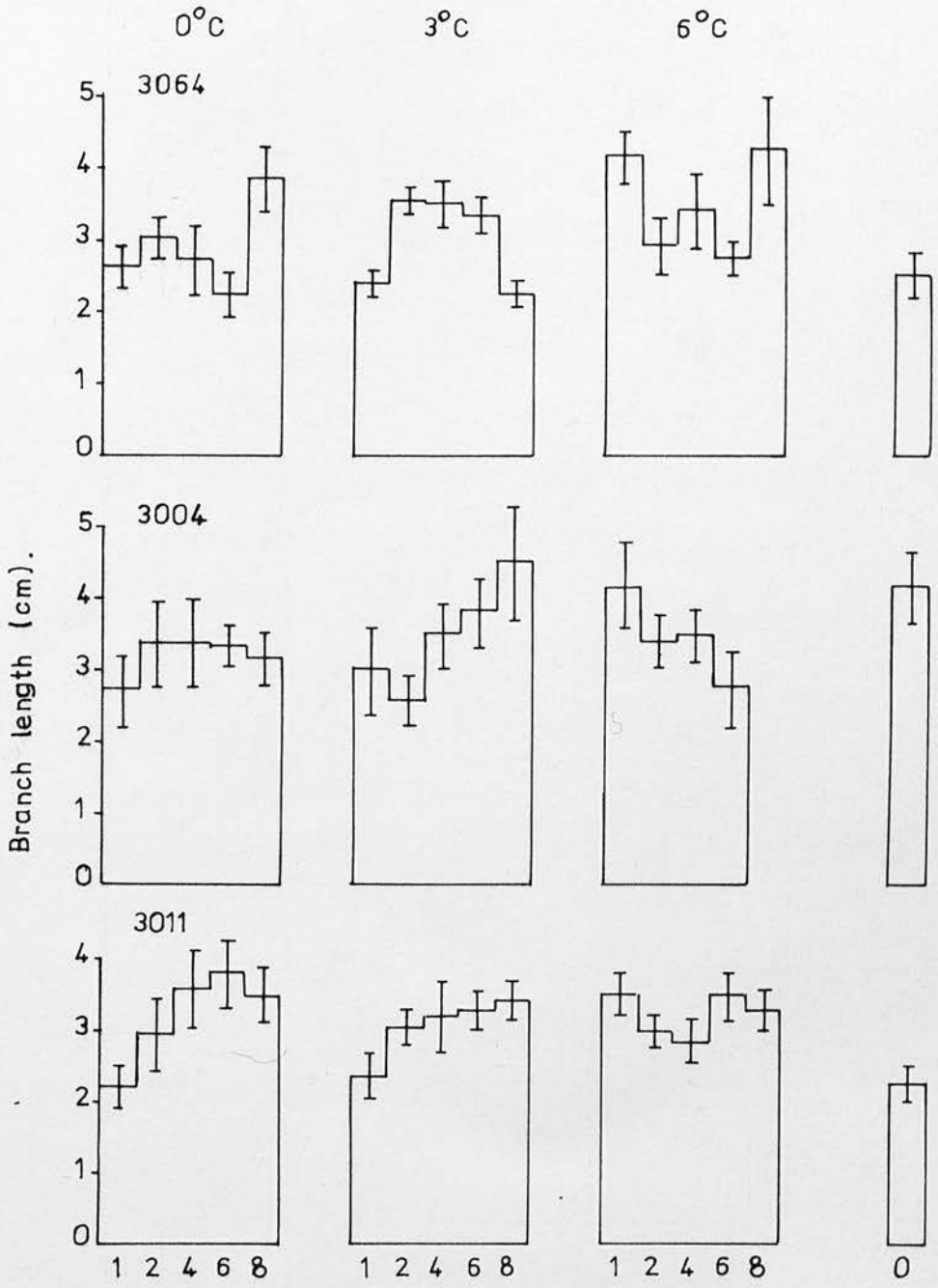
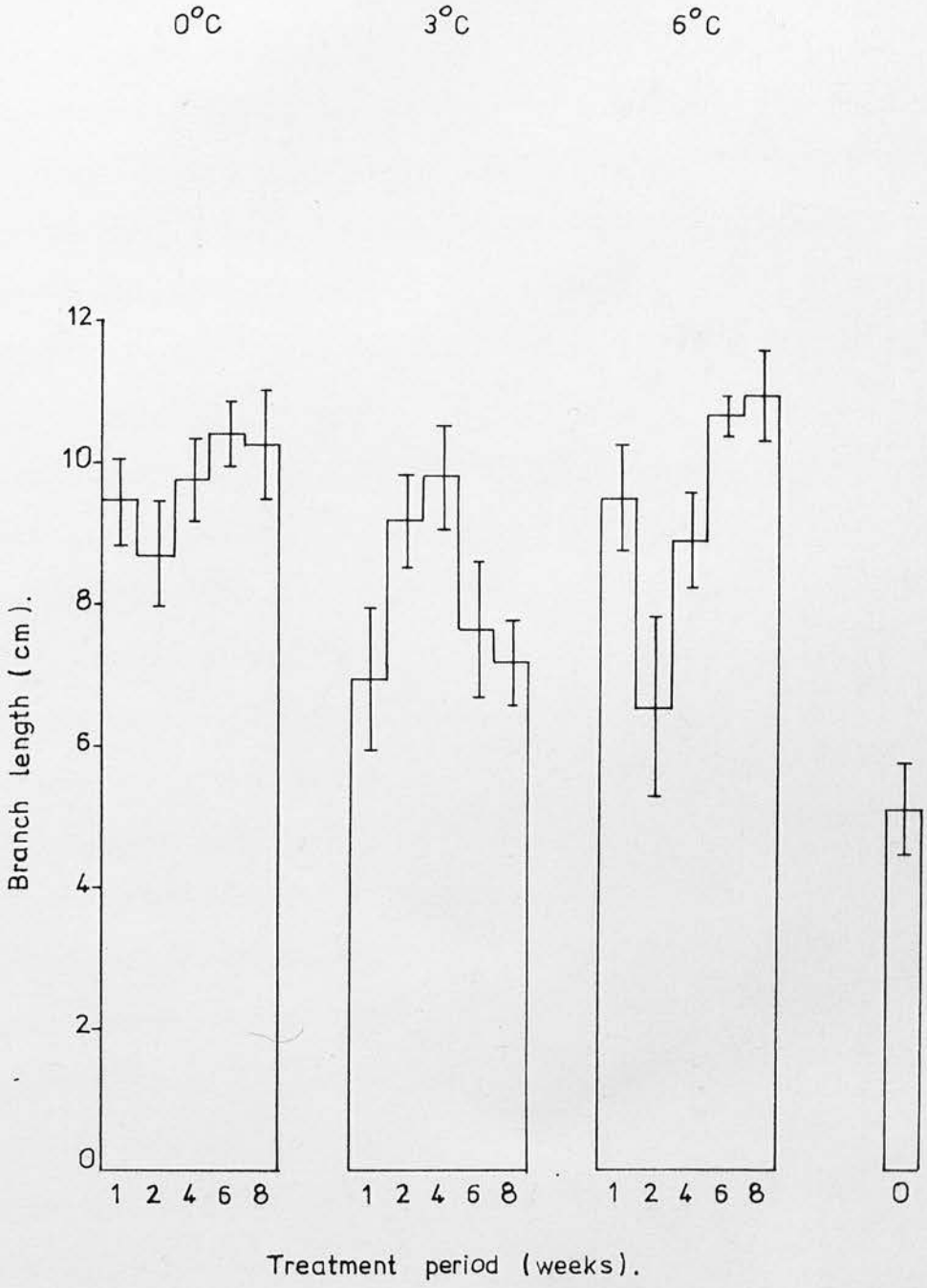


FIGURE 6:4 Branch lengths of Sitka spruce clone 8000 after chilling treatments.



effective. A chilling temperature of 6°C equally well broke dormancy compared to 0° and 3°C, indicating that the threshold temperature for Sitka spruce is not below 6°C. Chilling using a higher temperature might establish the actual threshold temperature. A temperature of 6°C seems a somewhat high threshold, when one considers that a threshold of 5° or 6°C is reported for the initiation of flushing (Roche 1969). Campbell and Sugano (1975) however, suggest that a temperature of 10°C may have acted simultaneously in chilling and flushing Douglas fir seedlings.

Variation in the time of flushing within a provenance X treatment was greatest after the shorter chilling treatments, indicating that the chilling requirements for some of the plants had not been fully satisfied.

Natural flushing has been shown to be related largely to temperature. Experiments on the chilling requirements of Douglas fir (van den Driessche 1975, Campbell and Sugano 1975) have shown that flushing and growth becomes possible over a wider range of temperature conditions as the breaking of dormancy becomes more complete, due to continued chilling. As was shown in Chapter 3, flushing was drastically delayed at low temperature and it is probably true to say that flushing would have been more rapid in those plants subjected to 6 and 8 weeks chilling had the warm temperature in the greenhouse been maintained.

The plants used in this experiment were out of doors until early October, by which time they may just have

received some chilling. If this was the case the removal of the plants to a heated greenhouse prior to the chilling treatments may have nullified any natural chilling. The timing and rate of flushing of control plants was considerably slower than those receiving 6 to 8 weeks chilling, but in some provenances was not disimilar to the response after 1 or 2 weeks chilling. It is unfortunate that only one photoperiod regime could be used after chilling. If a shorter photoperiod had been included in the experiment it would have been possible to show if a long photoperiod in part compensated for insufficient chilling in this species. The number of replicates required statistically prevented the use of two photoperiods, since with eight groups of plants involved the total number of plants was already 1,200.

Farrar (1961) and Nienstaedt (1966) have shown that the age of the bud affects the chilling requirements of Picea species. Long photoperiods are more effective in breaking the dormancy of immature buds (July) than older buds (September), as immediately after budset dormancy is relatively mild. Nienstaedt also found that immature buds exposed to chilling in late July require more chilling (6 - 8 weeks) than the fully developed September buds (4 - 6 weeks). The setting of buds of the provenance seedlings used here will have followed a clinal trend in response to decreasing daylength. The time interval between bud set of northern and southern provenances at Bush, Midlothian has been shown to be about 41 days (Kraus and

Lines 1976), with the most southerly provenances forming buds in late October. The age of the buds and the degree of dormancy obtained should therefore follow a clinal trend with latitude. No clinal trend in chilling requirement was found in these provenance seedlings, possibly because the difference in age of the buds was too small and, or, because all provenances had reached the dormant - steady state of Smith and Kefford (1964). Farrar (1961) noted that there were no consistent differences in chilling requirement between seed sources, while Nienstaedt (1967) believed northern cold-climate sources of Picea species required more chilling than southern sources. The time to complete flushing of control plants of Sitka spruce agrees with Farrar's (1961) results for Norway spruce.

Shoot extension was not directly affected by chilling treatment - if this had been so one might have expected a stepwise increase in height gain with increasing chilling. This result indicates that chilling does not affect the expression of the primordia laid down in the bud.

Considering the photoperiodic conditions in the greenhouse were constant during the experiment and the temperature conditions were minimum 11°C, maximum 20°C in April, and 15°/25°C in May, it is surprising that plants sufficiently chilled had ceased growth by early June after 10-12 weeks growth. The long photoperiod and warm temperatures are conditions conducive to 'free' growth, yet northern provenances did not respond. The cooler

temperatures earlier in the experiment may be partly responsible for this. The growth response of southern provenances was probably a clinal trend rather than irregular free growth.

Apical control in P. sitchensis has been demonstrated by Cannell (1974) and in P. glauca by Fraser (1962). The degree of apical control of shoot growth often changes with physiological tree age, but results for these seedlings oppose apical dominance. The lengths of branches of the current season whorl were surprisingly long and generally exceeded leader extension. Results for the ratio of lateral to leader length are 128 - 163%,* in contrast to those found for 8 year-old Sitka spruce of 33 - 63% (Cannell 1974). That long branches subtend long leaders however, reflects the findings of Cannell. Only provenance 3032 and clone 8000 showed any tendency towards apical dominance with lateral/leader ratios of 96% and 95% respectively.

The loss of a large number of plants in the 8 week x 6°C treatment affected statistical analysis. Respiration at 6°C could create a negative energy balance and it would seem that plants at this temperature for a long period continued respiration with consequent weakening. Indeed Doorenbos (1953) and Vegis (1964) have mentioned several researchers who observed increases in respiration during chilling.

* except provenance 3032 and clone 8000

CHAPTER 7. DISCUSSION AND CONCLUSIONS.

When studying the vegetative growth cycle of any species it is difficult to separate phases of that cycle for experimentation, for not only are the growth phases interrelated but environmental influences are also interdependent. This has been made evident in the experiments carried out here and by many other workers (e.g. Heide 1974b, Dormling et al. 1968).

The most important factor influencing shoot growth in northern coniferous species is the morphogenetic phase of bud development (van den Berg and Lanner 1971). Vegetative buds of Sitka spruce pass through three phases of development :- 1) a resting or dormant phase, 2) a period of shoot elongation and bud-scale formation and 3) needle primordial formation (Burley 1966a). The amount of growth made is closely related to the numbers of needle primordia laid down in the winter bud (Burley 1966b, Cannell 1974). The duration of deposition not only varies with provenance, but has been shown to be influenced by temperature in white spruce and black spruce (Pollard and Logan 1977).

In this study, bud formation throughout a range of Sitka spruce provenance seedlings was more rapid at warm temperatures than cool temperatures and the observed latitudinal trend in the timing of bud formation is consequent on the time of growth cessation. Burley (1966b) reports similar findings and concluded that bud

formation is hastened by relatively high temperatures immediately after the critical daylength is reached.

The development of leaf primordia within the bud begins when bud-scale initiation ceases. Northern Sitka spruce provenances have been shown to deposit leaf primordia over a shorter period of time than southern provenances (Burley 1966a, Cannell and Willett 1975, Pollard et al. 1975), a possible adaptation to the period available for bud morphogenesis at the latitude of origin. Reports on provenance variation in rate of needle initiation are at variance; Cannell and Willett (1975) found rates to be similar for five provenances in the field, whereas Pollard et al. (1975) in a controlled environment describe a faster rate for northern provenances, compared to a slow initial rate in southern provenances. Nevertheless southern sources have been shown repeatedly to determine more needles than northern sources, which must be mainly a result of the duration of deposition. The difference in the timing of the sequence of events in bud development between seed sources, causes variation in the duration of growth. Considering the differing reports on the rate of bud development, further work on this topic, both in controlled environments and using older material from the field may clarify the situation.

Environmental conditions during primordial initiation in Norway spruce can affect the depth of dormancy attained, the conditions necessary to break dormancy and

the subsequent amount of growth (Dormling et al. 1968). The influence of environmental factors on the process of bud development in Sitka spruce remains to be investigated. Knowledge of the effects of temperature during the period of leaf initiation, for both the rapid, early phase and slower, later phase as described by Owens and Molder (1976), the response of different provenances to such temperature treatments and any variation in response with the age of the plant material is needed.

Dormancy in Sitka spruce is broken by increasing temperature, possibly interacting with lengthening photoperiod, after chilling. The amount of chilling required for uniform flushing and normal shoot growth of two-year old provenance seedlings was eight weeks at a temperature from 0°-6°C, with no apparent differences in demand between provenances. The effect of different photoperiods after chilling treatment and the interaction of photoperiod and flushing temperature needs to be studied.

The breaking of dormancy and the onset of bud growth in the spring is characterised by the swelling of buds or flushing. Diverse environmental factors influence flushing. In a controlled environment flushing was considerably retarded at 8°C, compared to either constant 20°C or a day/night temperature of $20^{\circ}/8^{\circ}$C. In a greenhouse the length of artificial chilling period affected the time of the start of flushing but had little

influence on the rate of flushing.

The start of flushing has been shown to be related to spring temperatures at the place of origin (Burley 1966b). Out of doors, provenance seedlings followed a latitudinal trend in time of flushing, with northern sources flushing earlier in response to cooler spring temperatures. This finding is in accordance with those of Burley (1966b) and Cannell and Willett (1975).

Provenance seedlings with buds matured at cool temperatures flushed before those matured at warmer temperatures, after overwintering out of doors. This result agrees with the demonstration by Dormling et al. (1968), of the important influence of environmental conditions during needle primordial initiation and is in agreement with the conclusion drawn by Heide (1974b) for Picea abies, that bud maturation at high temperatures induces a deeper state of dormancy than maturation at low temperatures.

Rate and duration of shoot extension are affected by temperature. From the experiments reported here, a day temperature of 20°C and night temperature of 8°-11°C, resulted in maximal growth for the majority of the plant types studied. A day/night temperature differential proved as good or better than constant 20°C, a useful result when planning controlled environment or artificial heating regimes.

Within a temperature regime, inherent differences between provenances in both rate and duration of shoot

extension have been shown and account for provenance variation in total height growth made.

Young seedlings of Sitka spruce are capable of free growth and can thus augment the flush of predetermined growth. Free growth was only evident in warm temperature conditions. More detailed work on the capacity of different provenance seedlings for free growth could be of value. The application of environmental conditions conducive to free growth in the raising of seedlings could produce a height differential in the early years, of profit to the forester.

Lammas flushes in some older plants also occurred at the warmer temperature regimes. Lammas flushes in the field are in response to favourable environmental conditions at the end of the growing season and these controlled environment results reflect the need for warm temperature conditions.

Growth cessation in Sitka spruce has been shown to be a response to decreasing daylength (Burley 1966b, Lines and Mitchell 1966) and is an adaptation to the environment at the source of origin, affording protection from lethal autumn frosts. The long latitudinal range of Sitka spruce has resulted in photoperiodic ecotypes which show a clinal trend of earlier growth cessation with increasing latitude; northern provenances having a longer critical daylength than southern provenances.

The experiment reported here however demonstrates

that photoperiod does not have absolute control over growth cessation. Temperature interacts with photoperiod so that low temperatures can induce growth cessation at relatively long daylengths, while warm temperatures appear to shorten the critical daylength. While daylength acts as a trigger for growth cessation in the field, adverse environmental conditions such as low temperatures could outweigh the effect of decreasing daylength. Low temperatures upset the commonly accepted latitudinal relationship between photoperiod and growth cessation in provenance seedlings, with southern sources more sensitive than provenances from the middle of the range.

It is acknowledged in the literature that one of the major factors affecting total height growth is the ability of young seedlings to make free growth and that free growth is dependent on the environment (Pollard and Logan 1975). Most of the plants used in the controlled environment rooms in the experiments reported here were still capable of free growth. Environmental influences on the growth of Sitka spruce may change with the age of the plant. The potential of the primordial shoot laid down in the overwintering bud, assumes increasing importance as a determinant of shoot growth with increasing age. The balance of the influence of temperature and photoperiod in the growth cycle may alter as growth becomes increasingly predetermined. Temperature during bud development will assume more importance.

Growth cessation of four-year old plants in the nursery was in response to decreasing daylength, as temperatures were still favourable. Natural environmental conditions at the end of the growing season may affect growth differently from year to year. In years of low temperatures, temperature may trigger growth cessation, while in warm summers decreasing daylength would have more influence.

Under controlled conditions one can determine exactly how morphogenesis is affected by specific environmental factors. Construction of models based on data obtained from plants growing in the open is difficult, because of the variability of natural environments. Models based on plants grown in growth rooms, can provide more precise descriptions of specific plant-environment interactions, even though the growth room phenotype studied may differ considerably from those grown in the field.

The differences in the morphology of the plants in the first experiment, illustrate how temperature can affect the development of predetermined needles and also the extension of stem units. At cool temperatures needle length and shoot extension were reduced and needle width increased, resulting in a plant form very different to that seen at warmer temperatures and also different to that found in the field.

Of necessity controlled environment experiments are

conducted on newly germinated seedlings, or as in this case, young transplants and clonal material, which may still be capable of free growth in suitable conditions. Older trees have predetermined annual growth and this age effect and the relationship between meristems responsible for shoot extension, leaf initial formation and cambial activity require further investigation before results of controlled environment experiments can be extrapolated to field conditions. The age effect is illustrated in the comparison of the growth of the diallel-cross progeny in the field and in the growth room. The genotypes reacted differently in the two environments.

Using controlled environments it would be possible to regulate the vegetative growth cycle of Sitka spruce in a similar manner to that demonstrated by Dormling et al. (1968) for Norway spruce. More research is necessary to determine the optimal treatments, especially at the end of the growing season, but a cycle might be composed as follows: four weeks of bud maturation in short days at a constant temperature (15^{o}-20^{o}C), eight weeks of dormancy with a chilling treatment, eight weeks of flushing and shoot extension at $20^{o}/8^{o}$C in long days and three weeks of budset at 20^{o}C in short days. The general aspect of completing the knowledge of environmental effects on the growth cycle of Sitka spruce is of importance, but more specifically the artificial ageing process would allow for the production of mature plant material for research

in a shortened time, of particular value to geneticists and plant breeders.

Intra-provenance variation in Sitka spruce has received little attention and any information gained has generally resulted from observations in inter-provenance studies. Considerable variation in height growth within a provenance X chilling treatment was seen in this study and intra-provenance variation in flushing (Lines 1964) and growth cessation (Pollard et al. 1975) has been reported. Studies of intra-provenance variation are necessary.

The experiments reported here have elucidated some of the effects of temperature on the growth cycle of Sitka spruce. The general influences of temperature on shoot extension growth have now been well investigated and the optimal temperature range is known. To interpret the physiological mechanism by which different temperature regimes affect growth, more must be known of their effect on properties such as leaf growth and rates of photosynthesis and respiration, and whether such rates vary with provenance. The importance of the correct humidity conditions for Sitka spruce in controlled environment studies cannot be understated.

The interaction of temperature and daylength on growth cessation has been clarified and the environmental conditions employed were fairly comprehensive. The timing

of the decreasing photoperiod appears to have been in line with the time lag in perception by the plants. It would be interesting to repeat this experiment with more mature plants, beyond the potential for free growth.

The chilling experiment results are not conclusive, mainly due to the drop in temperature in the greenhouse during the experiment. A repeat experiment therefore would be informative. A higher chilling temperature of 8^{o}-10^{o}C could be included, which might establish the threshold chilling temperature and also a longer chilling period, to determine if this could reduce the time to flushing.

The cessation of growth at long daylengths of northern provenances of Sitka spruce in the growth room, regardless of temperature regime, indicates their inability to utilise the full growing season if planted in Great Britain. No conclusions on the use of any particular provenance for general planting in this country can be drawn, but provenance 3032 from the Skeena/Nass Rivers region,a provenance possibly introgressed with white spruce, showed good height growth over a very short growing season and might be valuable for sites with a high frost risk.

The 1970 IUFRO collection of provenances is valuable research material and several investigations using these provenances have been made since the completion of the experimental work reported here. Further use of this material in research should be made.

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APPENDIX 3 - reference CHAPTER 3.

The effects of temperature on flushing and extension growth in a controlled environment.

A3:1 Growth room design.

General details and specifications.

Four growth chambers of the following description were available at the Forestry Commission Northern Research Station, Bush, Midlothian. For experiment 1 only two chambers were used, but all four were in use for the growth cessation experiment, Chapter 5.

Conviron growth chamber PGV-36

Shelf area	$3.3m^2$
Growth height	200cm.
Cubic capacity	$6.8m^3$
Max. light intensity	50,000 lux
Temperature range - lights on	$10^{\circ}-45^{\circ}C$
- lights off	$4^{\circ}-45^{\circ}C$
Temperature $^{\circ}C$ control	$\pm 0.5^{\circ}C$
Interior dimensions - width	246cm.
depth	216cm.
height	236cm.

Humidity - was controlled by a solid state resistance bridge amplifier and humidity sensor. Humidity was added by two centrifugal atomizing humidifiers. Humidity scale 30-100%.

Temperature switch - one growth room (number 2) was controlled by day/night dials, allowing a combination of two temperatures per day. The remaining three growth

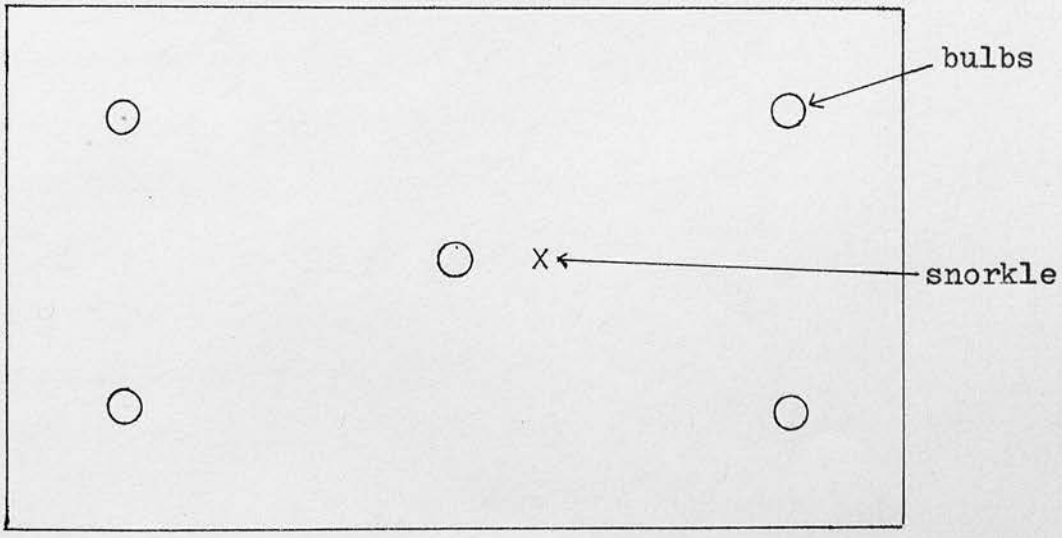
rooms had 24 temperature impulses per day, allowing for a temperature change every hour.

Lighting - Fluorescent tubes plus tungsten filament bulbs, Room temperature has an effect on the efficiency of the fluorescent tubes. The optimum light output changes very little with room temperatures between 15^{o}-25^{o}C, but decreases 12% when the room temperature is raised from 25^{o} to 35^{o}C.

A3:2 Balancing and use of growth rooms.

The growth rooms used in any experiment must be balanced for temperature, humidity, light intensity and air flow, both within each room and between rooms.

Temperature balance within a room was achieved in the following way: all light sources except the tungsten filament bulbs were turned off. The central bulb (as in plan below) was removed, and a calibrated thermometer inserted down a snorkle which was in a permanent position near the centre of the growth area, extending to a height of approximately 60 cm.



Plan: to show position of tungsten filament bulbs and snorkle in growth room. The position of the bulbs marks the five points where measurements are taken during balancing.

Air is always drawn out of the growth room down the snorkle, and hence over the thermometer. After an equilibration period of 10 min, the thermometer was read, whilst still partly down the snorkle, and as the cycle changed from cooling to heating. Any necessary adjustments are then made on the temperature setting dial and the process repeated until the temperatures required are accurate.

A Grant recorder with interchangeable thermistor probes was used to monitor temperature conditions in the growth rooms at varying light intensities, prior to the experiment. With only tungsten filament bulbs temperature control was $\pm$ 0.5°C, but with the fluorescent tubes temperature control was reduced to $\pm$ 2°C. Temperature differences between ground level and 60 cm.were slight: $\pm$ 0.5°C. Variation in temperature around the room was less in growth room 3 at 20°C ($\pm$ 0.5°C), than in the less sophisticated growth room 2 ($\pm$ 1.0°C) at 8°C. In darkness very little variation from the set temperature was found. The time lapse in the reduction of soil temperature in those pots transferred from 20°C day to 8°C night was as follows: after 25 min. soil temperature = 18°C, after 1 hour 10 min. = 12°C, and after 2 hour 20 min. = 9°C. Temperature in the growth rooms was checked every day.

Humidity balance.

After setting the required humidity and allowing 10 - 15 min. equilibration, humidity levels were checked using a wet/dry

sling hygrometer, when the cycle was changing from cooling to heating. This process was repeated until the required humidity levels were obtained. Humidity was checked weekly throughout the experiment.

Light intensity balance.

Light readings were taken using an EEL portable photo-electric photometer at the five positions in both growth rooms, at the required temperatures. The results were compared between rooms, and if the levels were the same ratio around the rooms, but different intensities, the light canopies were raised or lowered until the intensity at floor level was the same in both rooms. If the ratios were not comparable, the lowest intensity cabinet was taken as a base and the ratio of the other cabinet altered by replacing tubes, until the levels were equal in both rooms. Light intensity under bright fluorescent lights was 16,500 lux at ground level and increased to 18,000 lux at 60 cm. The tungsten filament bulbs produced 85 lux at ground level and 100 lux at 60 cm. Variation around the rooms was slight, with daylight bulbs $\pm$ 5 lux, and fluorescent tubes $\pm$ 500 lux.

Air flow balance.

Readings were taken with an anemometer at a height of approximately 30 cm, in the five positions marked and for intervals of 1 min. Wind speed could be altered by adjusting the tension of fan belts. Air flow over the room was not expected to be equal (a deficiency in the

design of the growth rooms), and was found to vary $\pm$ 0.01 ms^{-1}. After balancing the growth rooms for airflow, checks on the relative humidity were made to ensure levels had not been altered.

Graphs on the outside of the growth rooms gave a continuous record of wet and dry bulb temperatures, so that any fault or irregularity could be seen at a glance, regardless of the time of day or night it occurred.

A3.3. Additional data - Tables overpage.

TABLE A3:1. Length of time (days) for stages in flushing and corresponding heat sum (≥5°c).

		8000	8014	AD	AG	HG	KH	CK
START	20	9.0 3240	8.0 2880	10.4 3744	9.8 3528	10.0 3600	11.0 3960	11.4 4104
	20/8	9.0 2484	8.3 2290	10.6 2926	11.6 3202	10.8 2981	11.8 3257	11.2 3091
	8	15.3 1102	14.3 1030	31.2 2246	32.0 2304	30.4 2189	32.0 2304	34.0 2448
Terfin	20	17.2 6192	15.2 5472	18.4 6624	22.4 8064	14.3 5148	21.6 7776	22.8 8208
	20/8	18.8 5189	18.2 5023	21.0 5796	25.0 6900	20.2 5573	27.0 7452	26.0 7176
	8	46.0 3312	37.7 2714	57.0 4104	67.4 4853	57.8 4162	61.5 4428	59.5 4284
Terdur	20	8.2 2952	7.2 2592	8.0 2880	12.6 4536	6.0 2160	10.6 3816	11.4 4104
	20/8	9.8 2705	9.8 2705	10.7 2953	13.4 3698	9.4 2594	15.2 4195	14.8 4085
	8	30.7 2210	23.3 1678	26.7 1922	35.4 2549	29.4 2117	28.8 2074	28.5 2052
Totfin	20	17.2 6192	21.2 7632	20.8 7488	24.2 8712	14.7 5292	23.2 8352	25.5 9180
	20/8	19.3 5327	22.7 6265	23.0 6348	26.8 7397	22.8 6293	28.0 7728	30.4 8390
	8	47.8 3442	48.2 3470	62.8 4522	67.4 4853	57.9 4169	66.3 4774	59.5 4284
Totdur	20	8.2 2952	13.2 4752	10.4 3744	14.4 5184	6.3 2268	12.2 4392	14.1 5076
	20/8	10.3 2843	14.4 3974	12.4 3422	15.2 4195	12.0 3312	16.2 4471	19.2 5299
	8	32.5 2340	33.9 2441	31.6 2275	35.4 2549	29.5 2124	32.3 2326	28.5 2052

TABLE A3:2. Parameter 'C' of the Gompertz equation, as fitted to the growth data.

	AD	AG	HG	KH	CK
20	13.91	19.57	21.15	20.23	12.45
20/8	14.99	14.42	21.88	20.36	13.97
8	8.78	7.87	4.85	11.27	7.90

TABLE A3:3. Supplementary variables measured at end of Experiment 1.

			8000	8014	AD	AG	HG	KH	CK
	1972 LEADER	20	4.1	4.0	4.4	3.4	3.4	3.5	2.7
i)	DIAMETER GAIN	20/8	4.1	3.9	3.5	3.8	3.9	3.8	3.3
	(mm)	8	2.5	3.0	1.4	1.4	1.1	1.5	1.2
	BRANCH LENGTH	20	12.9	9.4	7.6	10.0	10.9	13.2	9.1
ii)	1972 ORIGIN	20/8	13.8	9.0	10.1	11.1	11.4	10.2	9.7
	(cm)	8	12.4	8.5	5.7	5.4	5.2	6.7	5.5
	TOTAL NO.	20	5.5	5.7	4.1	4.0	4.5	6.4	2.7
iii)	BUDS BRANCH	20/8	6.5	6.7	6.1	5.8	6.5	5.0	3.2
	1972 ORIGIN	8	3.3	4.6	1.6	1.1	1.1	1.7	1.7

Levels of significance ** $p \leq 0.01$
* $p \leq 0.05$ (Tukey's test).

	CLONES	TEMPERATURE	PROGENY	TEMPERATURE
i)	ns	20 20/8 8 **	AD KH AG HG CK **	20 20/8 8 **
ii)	**	ns	KH HG AG CK AD **	20 20/8 8 **
iii)	ns	**	KH HG AD AG CK *	20 20/8 8 **

TABLE A3:4. Analysis of variance tables.

Flushing Stage - Clones (Reference Table 3: 4).

1) Variate = Start

Source of Variation	DF	SS	MS	VR	F 5%	F 1%
Clones	1	7.11	7.11	35.56	4.17	7.56
Temperature	2	312.67	156.33	781.67	3.32	5.39
Interaction	2	0.22	0.11	0.56	(3.32)	(5.39)
Residual	30	6.00	0.20			
Total	35	325.99	9.31			

2) Variate = Terfin

Clones	1	121.00	121.00	9.74	4.17	7.17
Temperature	2	4834.66	2417.33	194.60	3.32	5.39
Interaction	2	100.67	50.33	4.05	3.32	(5.39)
Residual	30	372.67	12.42			
Total	35	5428.99	155.11			

3) Variate = Terdur

Clones	1	69.44	69.44	6.16	4.17	(7.56)
Temperature	2	2692.66	1346.33	119.50	3.32	5.39
Interaction	2	94.89	47.44	4.21	3.32	(5.39)
Residual	30	338.00	11.27			
Total	35	3195.00	91.29			

4) Variate = Totfin

Clones	1	58.78	58.78	6.25	4.17	(7.56)
Temperature	2	6254.88	3127.44	332.71	3.32	5.39
Interaction	2	22.89	11.44	1.22	(3.32)	(5.39)
Residual	30	282.00	9.40			
Total	35	6618.54	189.10			

5) Variate = Totdur

Source of Variation	DF	SS	MS	VR	F 5%	F 1%
Clones	1	106.78	106.78	12.88	4.17	7.56
Temperature	2	3772.22	1886.11	227.55	3.32	5.39
Interaction	2	21.56	10.78	1.30	(3.32)	(5.39)
Residual	30	248.67	8.29			
Total	35	4149.22	118.55			

6) Variate = Seqfin

Clones	1	348.44	348.44	78.40	4.17	7.56
Temperature	2	94.89	47.44	10.67	3.32	5.39
Interaction	2	32.89	16.44	3.70	3.32	(5.39)
Residual	30	133.33	4.44			
Total	35	609.55	17.42			

Flushing Stage - Progeny (Reference Table 3:4)

7) Variate = Start

Progeny	4	29.82	7.45	0.85	(2.54)	(3.68)
Temperature	2	7406.62	3703.31	423.88	3.17	5.01
Interaction	8	19.39	2.42	0.28	(2.11)	(2.85)
Residual	56	489.26	8.74			
Total	70	7945.08	113.50			

8) Variate = Terfin

Progeny	4	606.98	151.75	5.78	2.57	3.76
Temperature	2	25257.75	12628.88	481.42	3.20	5.10
Interaction	8	176.30	22.04	0.84	(2.14)	(2.92)
Residual	46	1206.70	26.23			
Total	60	27247.73	454.13			

9) Variate = Terdur

Source of Variation	DF	SS	MS	VR	F 5%	F 1%
Progeny	4	329.72	82.43	4.86	2.57	3.76
Temperature	2	5846.32	2923.16	172.43	3.20	5.10
Interaction	8	164.00	20.50	1.21	(2.14)	(2.92)
Residual	46	779.83	16.95			
Total	60	7119.86	118.66			

10) Variate = Totfin

Progeny	4	631.60	157.90	4.61	2.56	3.72
Temperature	2	25420.01	12710.00	370.72	3.18	5.06
Interaction	8	290.75	36.34	1.06	(2.13)	(2.88)
Residual	49	1679.94	34.28			
Total	63	28022.29	444.80			

11) Variate = Totdur

Progeny	4	311.58	77.90	3.41	2.56	(3.72)
Temperature	2	5693.54	2846.77	124.57	3.18	5.06
Interaction	8	223.42	27.93	1.22	(2.13)	(2.88)
Residual	49	1119.79	22.85			
Total	63	7348.32	116.64			

12) Variate = Seqfin

Progeny	4	21.66	5.42	0.99	(2.57)	(3.76)
Temperature	2	53.87	26.94	4.94	3.20	(5.10)
Interaction	8	41.74	5.22	0.96	(2.14)	(2.91)
Residual	45	245.17	5.45			
Total	59	362.44	6.14			

Growth Stages and Height Gain (Reference Table 3:5)

Clones

13) Variate = Start

Source of Variation	DF	SS	MS	VR	F 5%	F 1%
Clones	1	3.36	3.36	30.83	4.22	7.72
Temperature	2	86.71	43.36	397.86	3.37	5.53
Interaction	2	0.72	0.36	3.31	(3.37)	(5.53)
Residual	26	2.83	0.11			
Total	31	93.63	3.02			

14) Variate = End

Clones	1	325.75	325.75	219.92	4.26	7.82
Temperature	2	41.68	20.84	14.07	3.40	5.61
Interaction	2	71.14	35.57	24.01	3.40	5.61
Residual	24	35.55	1.48			
Total	29	474.12	16.35			

15) Variate = Duration

Clones	1	257.61	257.61	162.92	4.26	7.82
Temperature	2	19.68	9.84	6.22	3.40	5.61
Interaction	2	81.64	40.82	25.82	3.40	5.61
Residual	24	37.95	1.58			
Total	29	396.88	13.69			

16) Variate = Height Gain

Clones	1	922.08	922.08	41.20	4.26	7.82
Temperature	2	186.16	93.08	4.16	3.40	(5.61)
Interaction	2	340.92	170.46	7.62	3.40	5.61
Residual	24	537.10	22.38			
Total	29	1986.27	68.49			

Growth Stages and Height Gain - Progeny (Reference Table 3: 5)

17) Variate = Start

Source of Variation	DF	SS	MS	VR	F 5%	F 1%
Progeny	4	6.49	1.62	33.16	2.56	3.72
Temperature	2	562.51	281.26	5742.23	3.18	5.06
Interaction	8	7.61	0.95	19.41	2.13	2.88
Residual	49	2.40	0.05			
Total	63	579.02	9.19			

18) Variate = End

Progeny	4	126.35	31.59	3.83	2.56	3.72
Temperature	2	373.39	186.69	22.66	3.18	5.06
Interaction	8	102.99	12.87	1.56	(2.13)	(2.88)
Residual	49	403.73	8.24			
Total	63	1006.47	15.98			

19) Variate = Duration

Progeny	4	124.33	31.08	3.83	2.56	3.72
Temperature	2	85.42	42.71	5.26	3.18	5.06
Interaction	8	125.54	15.69	1.93	(2.13)	(2.88)
Residual	49	398.11	8.12			
Total	63	733.41	11.64			

20) Variate = Height Gain

Progeny	4	275.52	68.88	2.29	(2.56)	(3.72)
Temperature	2	1669.99	835.00	27.79	3.18	5.06
Interaction	8	226.63	28.33	0.94	(2.13)	(2.88)
Residual	49	1471.85	30.04			
Total	63	3644.00	57.84			

Morphological Variables - Clones (Reference Table 3: 8)

21) Variate = Number of growth points

Source of Variation	DF	SS	MS	VR	F 5%	F 1%
Clones	1	19920.5	19920.5	152.57	4.24	7.77
Temperature	2	22.4	11.2	0.09	(3.38)	(5.57)
Interaction	1	624.9	624.9	4.79	4.24	(7.77)
Residual	25	3264.2	130.6			
Total	29	23831.9	821.8			

22) Variate = Total number buds on leader

Clones	1	46.69	46.69	9.11	4.17	7.56
Temperature	2	457.17	228.58	44.58	3.32	5.39
Interaction	2	125.06	62.53	12.19	3.32	5.39
Residual	30	153.83	5.13			
Total	35	782.75	22.36			

23) Variate = Ratio Leader/No. buds

Clones	1	2.94	2.94	55.51	4.17	7.56
Temperature	2	3.25	1.62	30.71	3.32	5.39
Interaction	2	0.16	0.08	1.55	(3.32)	(5.39)
Residual	30	1.59	0.05			
Total	35	7.93	0.23			

24) Variate = 1973 Leader Diameter.

Clones	1	0.47	0.47	2.55	(4.17)	(7.56)
Temperature	2	1.75	0.88	4.72	3.32	(5.39)
Interaction	2	5.40	2.70	14.56	3.32	5.39
Residual	30	5.56	0.18			
Total	35	13.20	0.38			

25) Variate = Extension/Diameter of Leader.

Source of Variation	DF	SS	MS	VR	F 5%	F 1%
Clones	1	70.47	70.47	49.98	4.17	7.56
Temperature	2	2.96	1.48	1.05	(3.32)	(5.39)
Interaction	2	3.76	1.88	1.33	(3.32)	(5.39)
Residual	30	42.30	1.41			
Total	35	119.50	3.41			

26) Variate = Total buds on 1973 branch.

Clones	1	5.25	5.25	4.20	4.17	(7.56)
Temperature	2	80.08	40.04	32.02	3.32	5.39
Interaction	2	25.83	12.92	10.33	3.32	5.39
Residual	30	37.52	1.25			
Total	35	148.69	4.24			

27) Variate = 1973 branch length.

Clones	1	578.64	578.64	175.17	4.17	7.56
Temperature	2	190.89	95.44	28.89	3.32	5.39
Interaction	2	197.98	98.99	29.96	3.32	5.39
Residual	30	99.10	3.30			
Total	35	1066.61	30.47			

28) Variate = Dry weight 1973 branch.

Clones	1	0.09	0.09	4.20	4.17	(7.56)
Temperature	2	0.11	0.05	2.34	(3.32)	(5.39)
Interaction	2	0.47	0.24	10.17	3.32	5.39
Residual	30	0.70	0.02			
Total	35	1.38	0.04			

29) Variate = Needle length.

Source of variation	DF	SS	MS	VR	F 5%	F 1%
Clones	1	0.06	0.06	4.13	(4.24)	(7.77)
Temperature	2	0.06	0.03	1.92	(3.38)	(5.57)
Interaction	1	0.01	0.01	0.70	(4.24)	(7.77)
Residual	25	0.39	0.01			
Total	29	0.52	0.02			

30) Variate = Dry weight 100 needles.

Clones	1	0.01	0.015	10.88	4.17	7.56
Temperature	2	0.19	0.100	68.09	3.32	5.39
Interaction	2	0.02	0.010	6.71	3.32	5.39
Residual	30	0.04	0.001			
Total	35	0.27	0.008			

Morphological Variables - Progeny (Reference Table 3:8)

31) Variate = Number of growth points.

Progeny	4	3490.0	872.5	5.84	2.62	3.86
Temperature	1	101.2	101.2	0.67	(4.10)	(7.35)
Interaction	4	294.6	73.6	0.49	(2.62)	(3.86)
Residual	37	5529.6	149.4			
Total	46	9415.4	204.7			

32) Variate = Total number of buds on leader.

Progeny	4	123.12	30.78	2.38	(2.54)	(3.68)
Temperature	2	1357.48	678.74	52.45	3.17	5.01
Interaction	8	261.82	32.73	2.53	2.11	(2.85)
Residual	57	737.62	12.94			
Total	71	2480.04	34.93			

33) Variate = Ratio Leader/No. of buds.

Source of variation	DF	SS	MS	VR	F 5%	F 1%
Progeny	4	5.36	1.34	6.36	2.54	3.68
Temperature	2	3.05	1.52	7.24	3.17	5.01
Interaction	8	1.77	0.22	1.05	(2.11)	(2.85)
Residual	57	12.01	0.21			
Total	71	22.19	0.31			

34) Variate = 1973 Leader Diameter

Progeny	4	2.15	0.54	2.02	(2.52)	(3.65)
Temperature	2	7.43	3.72	13.96	3.15	4.98
Interaction	8	3.09	0.38	1.45	(2.10)	(2.82)
Residual	58	15.45	0.26			
Total	72	28.13	0.39			

35) Variate = Extension/Diameter of Leader.

Progeny	4	27.32	6.83	3.38	2.52	(3.65)
Temperature	2	110.36	55.18	27.29	3.15	4.98
Interaction	8	35.28	4.41	2.18	2.10	(2.82)
Residual	58	117.26	2.02			
Total	72	290.22	4.03			

36) Variate = Total buds on 1973 branch.

Progeny	4	116.72	29.18	8.06	2.52	3.65
Temperature	2	417.61	208.80	57.66	3.15	4.98
Interaction	8	84.57	10.57	2.92	2.10	2.82
Residual	58	210.04	3.62			
Total	72	828.95	11.51			

37) Variate = 1973 branch length.

Source of variation	DF	SS	MS	VR	F 5%	F 1%
Progeny	4	269.46	67.36	8.78	2.52	3.65
Temperature	2	1201.59	600.79	78.30	3.15	4.98
Interaction	8	135.26	16.91	2.20	2.10	(2.82)
Residual	58	445.00	7.67			
Total	72	2051.32	28.49			

38) Variate = Dry weight 1973 branch.

Progeny	4	0.88	0.22	6.70	2.52	3.65
Temperature	2	2.49	1.25	38.17	3.15	4.98
Interaction	8	0.30	0.04	1.14	(2.10)	(2.82)
Residual	58	1.89	0.03			
Total	72	5.57	0.08			

39) Variate = Needle length.

Progeny	4	1.08	0.27	5.01	2.54	3.68
Temperature	2	2.46	1.23	22.92	3.17	5.01
Interaction	8	0.39	0.05	0.91	(2.11)	(2.85)
Residual	57	3.06	0.05			
Total	71	6.99	0.09			

40) Variate = Dry weight 100 needles.

Progeny	4	0.07	0.019	9.51	2.52	3.65
Temperature	2	0.15	0.076	37.92	3.15	4.98
Interaction	8	0.05	0.006	3.21	2.10	2.82
Residual	58	0.11	0.002			
Total	72	0.39	0.005			

Additional Morphological Variables (Reference Appendix Table A3:2)

- Clones

41) Variate = 1972 Leader diameter gain.

Source of variation	DF	SS	MS	VR	F 5%	1%
Clones	1	0.08	0.08	0.25	(4.17)	(7.56)
Temperature	2	13.00	6.50	19.35	3.32	5.39
Interaction	2	0.99	0.49	1.48	(3.32)	(5.39)
Residual	30	10.08	0.33			
Total	35	24.17	0.69			

42) Variate = Branch length, 1972 origin.

Clones	1	149.86	149.86	43.86	4.17	7.56
Temperature	2	6.48	3.24	0.95	(3.32)	(5.39)
Interaction	2	2.86	1.43	0.42	(3.32)	(5.39)
Residual	30	102.50	3.41			
Total	35	261.71	7.47			

43) Variate = Total buds on branch, 1972 origin.

Clones	1	2.50	2.50	1.23	(4.17)	(7.56)
Temperature	2	42.12	21.06	10.32	3.32	5.39
Interaction	2	2.34	1.17	0.57	(3.32)	(5.39)
Residual	30	61.21	2.04			
Total	35	108.18	3.09			

Additional Morphological Variables (Reference Appendix Table A3:2).

- Progeny.

44) Variate = 1972 Leader diameter gain.

Source of variation	DF	SS	MS	VR	F 5%	1%
Progeny	4	4.00	1.00	3.86	2.52	3.65
Temperature	2	85.80	42.90	165.66	3.15	4.98
Interaction	8	4.93	0.61	2.38	2.10	(2.82)
Residual	58	15.02	0.26			
Total	72	109.75	1.52			

45) Variate = Branch length, 1972 origin.

Progeny	4	47.26	11.81	3.73	2.54	3.68
Temperature	2	356.57	178.28	56.40	3.17	5.01
Interaction	8	57.54	7.19	2.27	2.11	(2.85)
Residual	56	177.01	3.16			
Total	70	638.38	9.12			

46) Variate = Total buds on branch, 1972 origin.

Progeny	4	29.11	7.28	3.25	2.54	(3.68)
Temperature	2	205.39	102.69	45.91	3.17	5.01
Interaction	8	41.88	5.23	2.34	2.11	(2.85)
Residual	56	125.27	2.23			
Total	70	401.66	5.73			

APPENDIX 4 - reference Chapter 4.

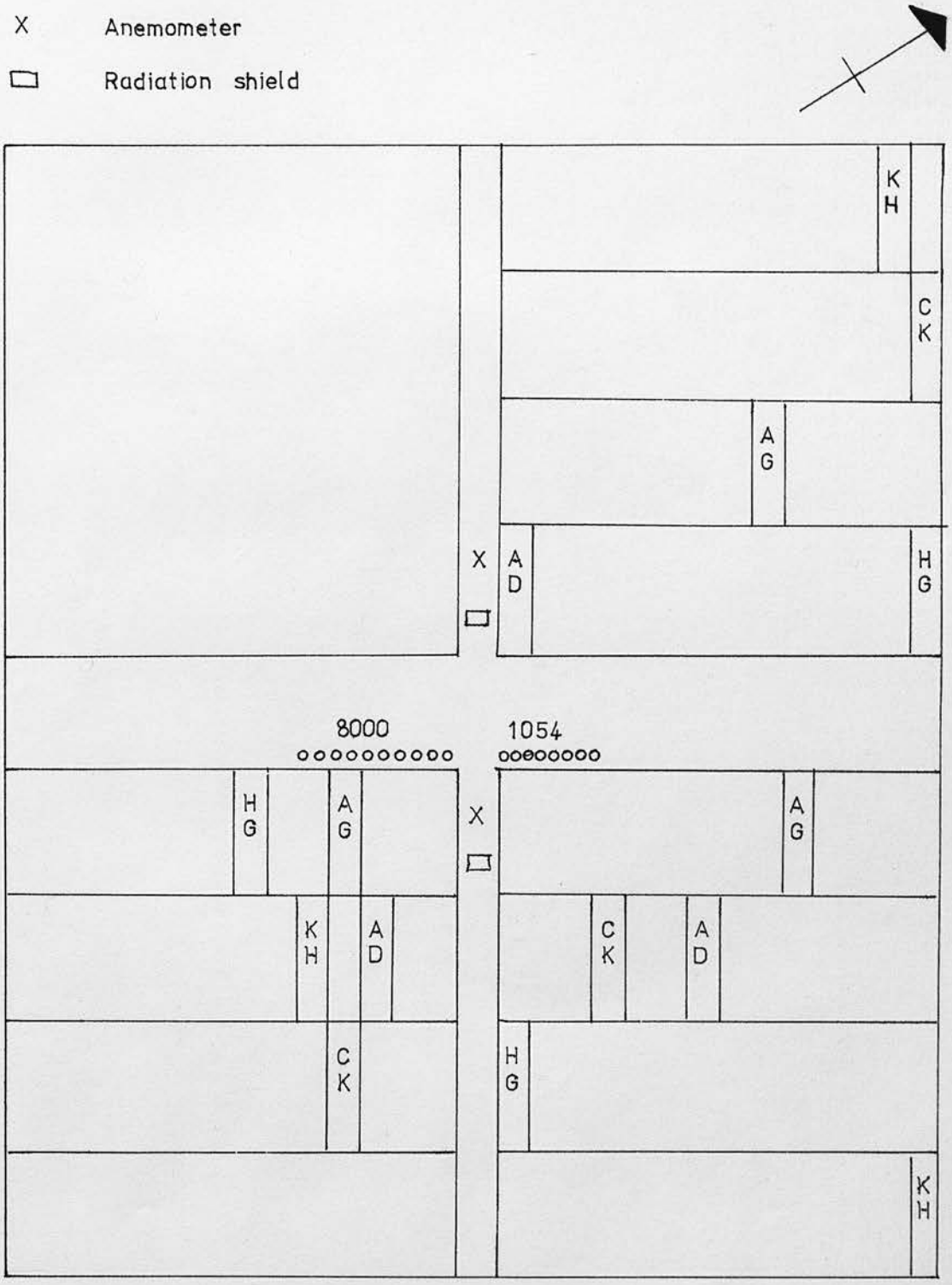
The seasonal growth of Sitka spruce in the field.

Plan A4: 1

4 plant line plots at 2m x 2m spacing.

X Anemometer

▭ Radiation shield



A4:2 Analysis of variance tables

Flushing stage - Progeny (Reference Table 4:2).

1) Variate = Terfin.

Source of Variation	DF	SS	MS	VR	F 5%	F 1%
Progeny	4	794.33	198.58	5.16	2.56	3.73
Residual	49	1885.28	38.48			
Total	53	2679.60	50.56			

2) Variate = Totfin

Progeny	4	500.07	125.02	3.78	2.54	3.68
Residual	55	1820.67	33.10			
Total	59	2320.73	39.33			

3) Variate = Seqfin

Progeny	4	33.50	8.38	0.59	(2.56)	(3.73)
Residual	49	691.09	14.10			
Total	53	724.60	13.67			

Flushing stage - Clone and graft

4) Variate = Terfin

'Clones'	1	1388.47	1388.47	156.48	4.49	8.53
Residual	16	141.98	8.87			
Total	17	1530.44	90.03			

Source of Variation	DF	SS	MS	VR	F 5%	F 1%
5) Variate = Totfin						
'Clones'	1	1484.34	1484.34	178.20	4.49	8.53
Residual	16	133.28	8.33			
Total	17	1617.61	95.15			
6) Variate = Seqfin						
'Clones'	1	1.60	1.60	0.47	(4.49)	(8.53)
Residual	16	54.90	3.43			
Total	17	56.50	3.32			
Growth stage - Progeny (Reference Table 4: 3)						
7) Variate = Start						
Progeny	4	1.44E	3.60E	-		
Residual	52	0.00E	0.00E			
Total	56	1.44E	2.57E			
8) Variate = Finish						
Progeny	4	63.95	15.99	5.27	2.56	3.72
Residual	50	151.74	3.04			
Total	54	215.68	3.99			
9) Variate = Duration						
Progeny	4	128.33	32.08	10.57	2.56	3.72
Residual	50	151.74	3.04			
Total	54	280.07	5.19			
10) Variate = Height gain						
Progeny	4	1202.95	300.74	3.65	2.56	(3.72)
Residual	50	4120.04	82.40			
Total	54	5322.98	98.57			

Source of Variation	DF	SS	MS	VR	F 5%	F 1%
Growth stage - Clone and graft						
11) Variate = Start						
'Clones'	1	1.78E	1.78E	-		
Residual	16	0.00E	0.00E			
Total	17	1.78E	1.05E			
12) Variate = Finish						
'Clones'	1	5.10	5.10	11.60	4.67	9.07
Residual	13	5.71	0.44			
Total	14	10.81	0.77			
13) Variate = Duration						
'Clones'	1	3.83	3.83	8.71	4.67	(9.07)
Residual	13	5.71	0.44			
Total	14	9.54	0.68			
14) Variate - Height gain						
'Clones'	1	33.55	33.55	2.91	(4.67)	(9.07)
Residual	13	149.91	11.53			
Total	14	183.46	13.10			

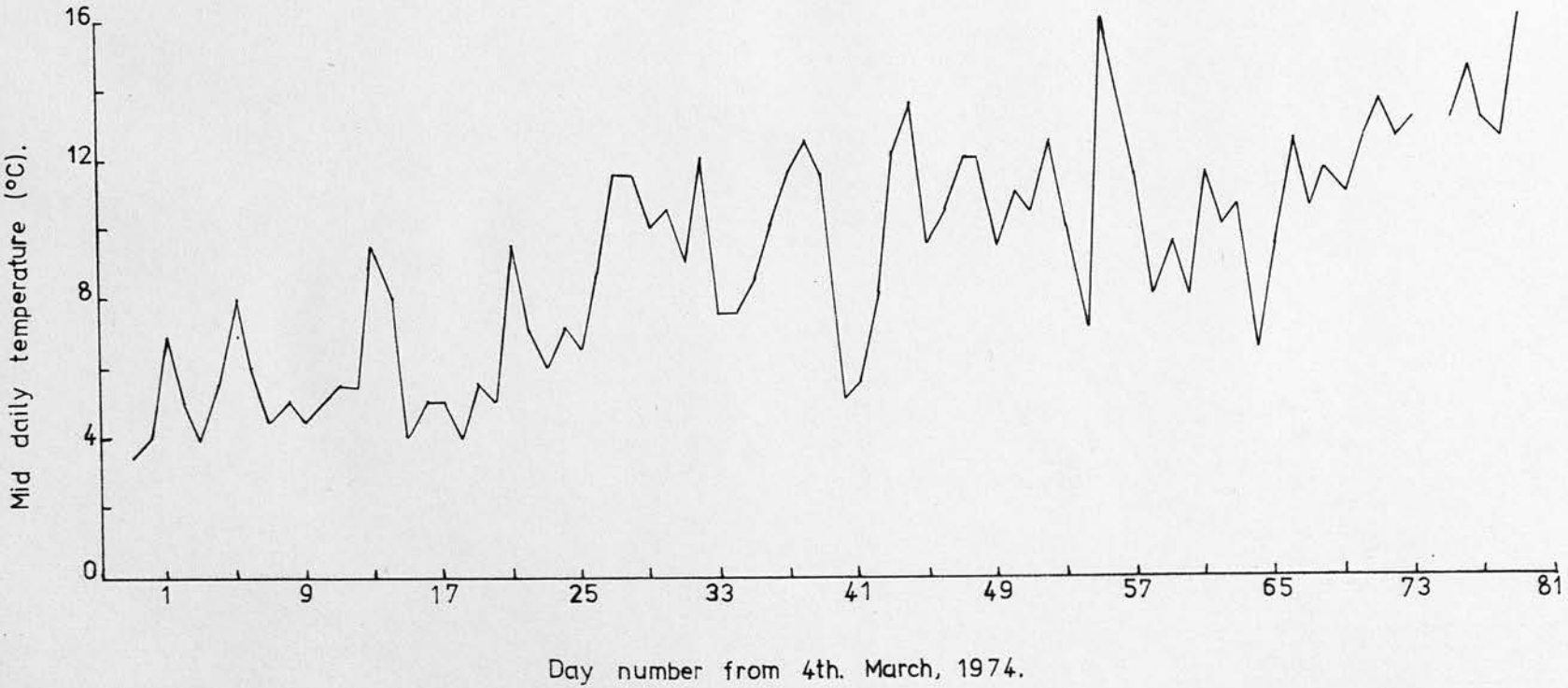
APPENDIX 5 - reference CHAPTER 5.

The influence of temperature on the cessation of height growth of Sitka spruce provenances.

FIGURE A5:1 Mid daily temperature at N.R.S., Bush, Midlothian, from minimum and maximum temperature records.

A5:2 Analysis of variance tables.

FIGURE A5:1 Mid daily temperature at N.R.S., Bush, Midlothian, from minimum and maximum temperature records. Day 1 = 4th. March, 1974.



APPENDIX 5 - re CHAPTER 5. Analysis of Variance tables.

Growth cessation - provenances.

1) Variate = Height gain at cessation of growth.

Source of Variation	DF	SS	MS	VR	F 5%	F 1%
Provenance	7	43.58	6.22	7.25	2.03	2.69
Temperature	3	297.19	99.06	115.29	2.62	3.83
Interaction	20	62.99	3.15	3.66	1.60	1.92
Residual	414	355.73	0.86			
Total	444	759.49	1.71			

2) Variate = Height gain at end of experiment.

Provenance	7	99.04	14.15	17.05	2.03	2.69
Temperature	3	262.29	87.43	105.36	2.62	3.83
Interaction	21	36.83	1.75	2.11	1.60	1.92
Residual	428	355.18	0.83			
Total	459	753.34	1.64			

3) Variate = Difference between Variates 1 and 2.

Provenance	7	16.93	2.42	21.34	2.03	2.69
Temperature	3	8.20	2.73	24.11	2.62	3.83
Interaction	20	9.87	0.49	4.35	1.60	1.92
Residual	414	46.92	0.11			
Total	444	81.93	0.18			

4) Variate = Time of growth cessation.

Provenance	7	102.31	14.61	5.05	2.03	2.69
Temperature	3	685.45	228.48	79.01	2.62	3.83
Interaction	20	484.97	24.25	8.38	1.60	1.92
Residual	387	1119.11	2.89			
Total	417	2391.85	5.73			

Growth cessation - clones.

5) Variate = Height gain at cessation of growth.

Source of Variation	DF	SS	MS	VR	F 5%	F 1%
Clones	1	2.44	2.44	2.67	(4.03)	(7.17)
Temperature	3	1.07	0.35	0.39	(2.79)	(4.20)
Interaction	3	5.54	1.85	2.02	(2.79)	(4.20)
Residual	52	47.40	0.91			
Total	59	56.45	0.95			

6) Variate = Height gain at end of experiment.

Clones	1	3.43	3.43	3.39	(4.03)	(7.17)
Temperature	3	1.24	0.41	0.41	(2.79)	(4.20)
Interaction	3	4.31	1.44	1.42	(2.79)	(4.20)
Residual	52	52.63	1.01			
Total	59	61.62	1.04			

7) Variate = Difference between variates 5 and 6.

Clones	1	0.08	0.08	0.84	(4.03)	(7.17)
Temperature	3	0.26	0.09	0.85	(2.79)	(4.20)
Interaction	3	0.39	0.13	1.30	(2.79)	(4.20)
Residual	52	5.26	0.10			
Total	59	6.00	0.10			

8) Variate = Time of growth cessation.

Clones	1	13.61	13.61	15.01	4.08	7.31
Temperature	3	15.19	5.06	5.59	2.84	4.31
Interaction	3	2.51	0.84	0.92	(2.84)	(4.31)
Residual	41	37.16	0.91			
Total	48	68.46	1.43			

Tukey's test - provenances not underscored by the same line are significantly different ($p \leqslant 0.01$).

Variate 1. Cessation height.

3032	3022	3050	3064	3059	3002	3013	3017

8^{o}	12^{o}	16^{o}	20^{o}

Variate 2. End height.

3032	3022	3064	3050	3002	3059	3013	3017

8^{o}	12^{o}	16^{o}	20^{o}

Variate 3. Difference in height.

3022	3032	3050	3059	3002	3064	3013	3017

Variate 4. Cessation time.

3032	3022	3050	3064	3059	3002	3013	3017

8^{o}	12^{o}	16^{o}	20^{o}

APPENDIX 6 - reference Chapter 6.

To define the minimum chilling requirements of Sitka spruce.

TABLE A6:1 Table of correlation coefficients for height gain and branch length (over page).

A6:2 Analysis of variance tables.

TABLE A6:1. Correlation coefficients for height gain and branch length.

		0°C					3°C					6°C				
	None	1	2	4	6	8	1	2	4	6	8	1	2	4	6	8
3028	0.864 **	0.907 **	0.731 *	0.975 **	0.961	0.843 **	0.936 **	0.891 **	0.853 **	0.875 **	0.869 **	0.823 **	0.620	0.881 **	0.983	-
3032	0.831 **	0.923	0.949 **	0.800 **	0.728 *	0.723 *	0.553	0.370	0.822 **	0.708 *	0.705 *	0.902 **	0.838 **	0.943 **	0.807 **	0.650
3053	0.677 *	0.451	0.756 *	0.901	0.780 **	0.968	0.437	0.730 *	0.401	0.660	0.802 **	0.869 **	0.060	0.907 **	0.905 **	-
3059	0.597	0.202	0.974 **	0.890 **	0.979 **	0.454	0.539	0.305	0.962 **	0.934 **	0.904 **	0.938 **	0.475	0.918 **	0.325	0.822 **
3064	0.560	0.502	0.779 **	0.960 **	0.882 **	0.953 **	0.825 **	0.327	0.813 **	0.828 **	0.826 **	0.643	0.251	0.949 **	0.793 *	0.724
3004	0.963	0.625	0.929	0.884	0.563	0.919	0.729	0.590	0.650	0.857	0.869	0.769	0.285	0.501	0.465	-
3011	0.451	0.734 *	0.766 *	0.764 *	0.590	0.704 *	0.862 **	0.577	0.720 *	0.922 **	0.552	0.566	0.715 *	0.881 **	0.920 **	0.915
8000	0.842 **	0.801 **	0.780 **	0.696 *	-	0.932	0.664 *	0.397	0.632 *	0.894 **	0.758 *	0.624	0.842 *	0.572	0.380	0.750 *

(** $p \leqslant 0.01$, * $p \leqslant 0.05$).

A6:2 Analysis of variance tables.

Flushing - whole experiment.

1) Variate = Days until subterminal started to flush.

Source of Variation	DF	SS	MS	VR	F 5%	F 1%
Provenance	6	30472.2	5078.7	44.28	2.10	2.82
Temperature	3	48115.7	16038.6	139.83	2.61	3.80
Weeks	5	297204.9	59441.0	518.22	2.22	3.04
Prov. x Temp.	18	6102.0	339.0	2.96	1.62	1.95
Prov. x Weeks	30	13032.4	434.4	3.79	1.47	1.71
Temp. x Weeks	7	1653.8	236.3	2.06	2.02	(2.66)
Prov. x Temp. x Weeks	41	13973.1	340.8	2.97	1.41	1.61
Residual	859	98528.6	114.7			
Total	969	509082.6	525.4			

2) Variate = Duration of subterminal flushing.

Provenance	6	15383.4	2563.9	3.63	2.10	2.82
Temperature	3	4703.4	1567.8	2.22	(2.61)	(3.80)
Weeks	5	14209.4	2841.9	4.02	2.22	3.04
Prov. x Temp.	18	9593.1	532.9	0.75	(1.62)	(1.95)
Prov. x Weeks	30	9945.9	331.5	0.47	(1.47)	(1.71)
Temp. x Weeks	7	11711.7	1673.1	2.37	2.02	(2.66)
Prov. x Temp. x Weeks	41	40282.6	982.5	1.39	(1.41)	(1.61)
Residual	859	607624.2	707.4			
Total	969	713453.6	736.3			

3) Variate = Days until terminal started to flush.

Source of Variation	DF	SS	MS	VR	F 5%	F 1%
Provenance	6	43781.1	7296.8	33.06	2.10	2.82
Temperature	3	107988.8	35996.3	163.11	2.61	3.80
Weeks	5	505304.4	101060.9	457.94	2.22	3.04
Prov. x Temp.	18	6164.8	342.5	1.55	(1.62)	(1.95)
Prov. x Weeks	30	6586.0	219.5	0.99	(1.47)	(1.71)
Temp. x Weeks	7	3503.3	500.5	2.27	2.02	(2.66)
Prov. x Temp. x Weeks	41	28392.1	692.5	3.14	1.41	1.61
Residual	857	189127.8	220.7			
Total	967	890848.1	921.2			

4) Variate = Duration of terminal flushing.

Provenance	6	2059.47	343.3	4.08	2.10	2.82
Temperature	3	5714.68	1904.9	22.62	2.61	3.80
Weeks	5	9435.81	1887.2	22.42	2.22	3.04
Prov. x Temp.	18	5979.52	332.2	3.95	1.62	1.95
Prov. x Weeks	30	4584.30	152.8	1.82	1.47	1.71
Temp. x Weeks	7	2117.59	302.5	3.59	2.02	2.66
Prov. x Temp. x Weeks	41	6577.00	160.4	1.91	1.41	1.61
Residual	857	72142.19	84.2			
Total	967	108610.56	112.3			

Flushing - Individual Provenances.

5) Variate = 3028. Days until subterminal started to flush.

Temperature	3	7300.49	2433.5	33.79	2.68	3.94
Weeks	5	53210.51	10642.1	147.78	2.29	3.17
Temp. x Weeks	7	1352.66	193.2	2.68	2.08	(2.79)
Residual	133	9578.07	72.0			
Total	148	71441.69	482.7			

6) Variate = 3028. Duration of subterminal flushing.

Source of variation	DF	SS	MS	VR	F 5%	F 1%
Temperature	3	3648.95	1216.3	17.54	2.68	3.94
Weeks	5	2175.47	435.1	6.27	2.29	3.17
Temp. x Weeks	7	1309.29	187.0	2.70	2.08	(2.79)
Residual	133	9224.42	69.4			
Total	148	16358.12	110.5			

7) Variate = 3028. Days until terminal started to flush.

Temperature	3	14299.1	4766.4	32.75	2.68	3.94
Weeks	5	70055.2	14011.0	96.26	2.29	3.17
Temp. x Weeks	7	3959.5	565.6	3.89	2.08	2.79
Residual	133	19359.0	145.6			
Total	148	107672.7	727.5			

8) Variate = 3028. Duration of terminal flushing.

Temperature	3	878.60	292.9	6.17	2.68	3.94
Weeks	5	310.80	62.2	1.31	(2.29)	(3.17)
Temp. x Weeks	7	481.85	68.8	1.45	(2.08)	(2.79)
Residual	133	6311.80	47.5			
Total	148	7983.05	53.9			

9) Variate = 3032. Days until subterminal started to flush.

Temperature	3	16156.76	5385.6	102.38	2.68	3.94
Weeks	5	70551.75	14110.4	268.22	2.29	3.17
Temp. x Weeks	7	1595.64	227.9	4.33	2.08	2.79
Residual	137	7207.09	52.6			
Total	152	95511.19	628.4			

10) Variate = 3032. Duration of subterminal flushing.

Source of variation	DF	SS	MS	VR	F 5%	F 1%
Temperature	3	109.71	36.6	0.65	(2.68)	(3.94)
Weeks	5	374.75	74.9	1.34	(2.29)	(3.17)
Temp. x Weeks	7	557.69	79.7	1.42	(2.08)	(2.79)
Residual	137	7679.23	56.1			
Total	152	8721.38	57.4			

11) Variate = 3032. Days until terminal started to flush.

Temperature	3	15512.96	5171.0	51.91	2.68	3.94
Weeks	5	65882.69	13176.5	132.28	2.29	3.17
Temp. x Weeks	7	1933.51	276.2	2.77	2.08	(2.79)
Residual	137	13646.55	99.6			
Total	152	96975.63	638.0			

12) Variate = 3032. Duration of terminal flushing.

Temperature	3	116.98	39.0	0.68	(2.68)	(3.94)
Weeks	5	475.34	95.1	1.65	(2.29)	(3.17)
Temp. x Weeks	7	468.43	66.9	1.16	(2.08)	(2.79)
Residual	137	7876.71	57.5			
Total	152	8937.45	58.8			

13) Variate = 3053. Days until subterminal started to flush.

Temperature	3	3021.8	1007.3	6.85	2.68	3.94
Weeks	5	40108.2	8021.6	54.51	2.29	3.17
Temp. x Weeks	7	3598.1	514.0	3.49	2.08	2.79
Residual	133	19572.5	147.2			
Total	148	66300.6	448.0			

14) Variate = 3053. Duration of subterminal flushing.

Source of Variation	DF	SS	MS	VR	F 5%	F 1%
Temperature	3	134.7	44.9	0.41	(2.68)	(3.94)
Weeks	5	1504.0	300.8	2.77	2.29	(3.17)
Temp. x Weeks	7	1073.6	153.4	1.41	(2.08)	(2.79)
Residual	133	14456.8	108.7			
Total	148	17169.1	116.0			

15) Variate = 3053. Days until terminal started to flush.

Temperature	3	11736.0	3912.0	14.44	2.68	3.94
Weeks	5	77296.6	15459.3	57.06	2.29	3.17
Temp. x Weeks	7	9252.7	1321.8	4.88	2.08	2.79
Residual	133	36035.5	270.9			
Total	148	134320.8	907.6			

16) Variate = 3053. Duration of terminal flushing.

Temperature	3	2264.31	754.8	7.96	2.68	3.94
Weeks	5	2470.19	494.0	5.21	2.29	3.17
Temp. x Weeks	7	1564.24	223.5	2.36	2.08	(2.79)
Residual	133	12607.00	94.8			
Total	148	18905.75	127.7			

17) Variate = 3059. Days until subterminal started to flush.

Temperature	3	9387.8	3129.3	24.12	2.68	3.94
Weeks	5	37817.8	7563.6	58.30	2.29	3.17
Temp. x Weeks	7	4386.4	626.6	4.83	2.08	2.79
Residual	138	17903.8	129.7			
Total	153	69495.7	454.2			

18) Variate = 3059. Duration of subterminal flushing.

Source of Variation	DF	SS	MS	VR	F 5%	F 1%
Temperature	3	2551.3	850.4	7.60	2.68	3.94
Weeks	5	2309.7	461.9	4.13	2.29	3.17
Temp. x Weeks	7	2565.5	366.5	3.27	2.08	2.79
Residual	138	15451.3	112.0			
Total	153	22877.7	149.5			

19) Variate = 3059. Days until terminal started to flush.

Temperature	3	23597.4	7865.8	27.67	2.68	3.94
Weeks	5	75262.6	15052.5	52.96	2.29	3.17
Temp. x Weeks	7	4926.1	703.7	2.48	2.08	(2.79)
Residual	136	38655.9	284.2			
Total	151	142441.9	943.3			

20) Variate = 3059. Duration of terminal flushing.

Temperature	3	1249.47	416.5	5.43	2.68	3.94
Weeks	5	2134.22	426.8	5.56	2.29	3.17
Temp. x Weeks	7	1483.05	211.9	2.76	2.08	(2.79)
Residual	136	10438.35	76.8			
Total	151	15305.09	101.4			

21) Variate = 3064. Days until subterminal started to flush.

Temperature	3	8807.8	2935.9	21.05	2.68	3.94
Weeks	5	33554.4	6710.9	48.11	2.29	3.17
Temp. x Weeks	7	1283.0	183.3	1.31	(2.08)	(2.79)
Residual	127	17715.4	139.5			
Total	142	61360.5	432.1			

22) Variate = 3064. Duration of subterminal flushing.

Source of Variation	DF	SS	MS	VR	F 5%	F 1%
Temperature	3	1607.0	535.7	3.40	2.68	(3.94)
Weeks	5	1898.6	379.7	2.41	2.29	(3.17)
Temp. x Weeks	7	1623.2	231.9	1.47	(2.08)	(2.79)
Residual	127	20021.1	157.6			
Total	142	25149.9	177.1			

23) Variate = 3064. Days until terminal started to flush.

Temperature	3	19617.6	6539.2	32.28	2.68	3.94
Weeks	5	57898.0	11579.6	57.16	2.29	3.17
Temp. x Weeks	7	3568.3	509.8	2.52	2.08	(2.79)
Residual	127	25729.8	202.6			
Total	142	106813.6	752.2			

24) Variate = 3064. Duration of terminal flushing.

Temperature	3	499.28	166.4	1.86	(2.68)	(3.94)
Weeks	5	1802.00	360.4	4.03	2.29	3.17
Temp. x Weeks	7	1103.81	157.7	1.76	(2.08)	(2.79)
Residual	127	11368.47	89.5			
Total	142	14773.55	104.0			

25) Variate = 3004. Days until subterminal started to flush.

Temperature	3	1182.9	394.3	2.10	(2.77)	(4.15)
Weeks	5	36805.6	7361.1	39.25	2.38	3.36
Temp. x Weeks	6	2087.4	347.9	1.86	(2.26)	(3.14)
Residual	57	10690.2	187.5			
Total	71	50766.0	715.0			

26) Variate = 3004. Duration of subterminal flushing.

Source of Variation	DF	SS	MS	VR	F 5%	F 1%
Temperature	3	758.8	252.9	1.13	(2.77)	(4.15)
Weeks	5	7194.9	1439.0	6.44	2.38	3.36
Temp. x Weeks	6	2005.2	334.2	1.50	(2.26)	(3.14)
Residual	57	12739.4	223.5			
Total	71	22698.2	319.7			

27) Variate = 3004. Days until terminal started flushing.

Temperature	3	10323.5	3441.2	13.65	2.77	4.15
Weeks	5	84068.6	16813.7	66.70	2.38	3.36
Temp. x Weeks	6	2415.6	402.6	1.60	(2.26)	(3.14)
Residual	57	14369.1	252.1			
Total	71	111176.6	1565.9			

28) Variate = 3004. Duration of terminal flushing.

Temperature	3	3111.03	1037.01	13.42	2.77	4.15
Weeks	5	3157.81	631.56	8.17	2.38	3.36
Temp. x Weeks	6	2140.01	356.67	4.62	2.26	3.14
Residual	57	4405.63	77.29			
Total	71	12814.47	180.49			

29) Variate = 3011. Days until subterminal started to flush.

Temperature	3	8279.7	2759.9	23.31	2.68	3.84
Weeks	5	37310.1	7462.0	63.02	2.29	3.17
Temp. x Weeks	7	1161.0	165.9	1.40	(2.08)	(2.79)
Residual	134	15866.2	118.4			
Total	149	62617.0	420.2			

30) Variate = 3011. Duration of subterminal flushing.

Source of Variation	DF	SS	MS	VR	F 5%	F 1%
Temperature	3	5521.0	1840.0	0.47	(2.68)	(3.94)
Weeks	5	9443.0	1889.0	0.48	(2.29)	(3.17)
Temp. x Weeks	7	43207.0	6172.0	1.57	(2.08)	(2.79)
Residual	134	528019.0	3940.0			
Total	149	586189.0	3934.0			

31) Variate = 3011. Days until terminal started to flush.

Temperature	3	18969.1	6323.0	20.49	2.68	3.94
Weeks	5	81336.4	16267.3	52.72	2.29	3.17
Temp. x Weeks	7	5855.8	836.5	2.71	2.08	(2.79)
Residual	134	41350.9	308.6			
Total	149	147512.2	990.0			

32) Variate = 3011. Duration of terminal flushing.

Temperature	3	3475.0	1158.3	8.11	2.68	3.94
Weeks	5	3613.9	722.8	5.06	2.29	3.17
Temp. x Weeks	7	1504.4	214.9	1.51	(2.08)	(2.79).
Residual	134	19129.2	142.8			
Total	149	27722.4	186.1			

Flushing - Clone 8000.

33) Variate = 8000. Days until subterminal started to flush.

Temperature	3	16580.2	5526.7	47.79	2.68	3.94
Weeks	5	22650.0	4530.0	39.17	2.29	3.17
Temp. x Weeks	7	2980.5	425.8	3.68	2.08	2.79
Residual	130	15034.0	115.6			
Total	145	57244.8	394.8			

34) Variate = 8000. Duration of subterminal flushing.

Source of Variation	DF	SS	MS	VR	F 5%	F 1%
Temperature	3	1734.87	578.3	5.97	2.68	3.94
Weeks	5	2776.82	555.4	5.74	2.29	3.17
Temp. x Weeks	7	4961.51	708.8	7.32	2.08	2.79
Residual	129	12487.46	96.8			
Total	144	21960.66	152.5			

35) Variate = 8000. Days until terminal started to flush.

Temperature	3	17279.4	5759.8	44.93	2.68	3.94
Weeks	5	47827.2	9565.4	74.62	2.29	3.17
Temp. x Weeks	7	4197.2	599.6	4.68	2.08	2.79
Residual	131	16793.4	128.2			
Total	146	86097.1	589.7			

36) Variate = 8000. Duration of terminal flushing.

Temperature	3	1760.13	586.7	10.77	2.68	3.94
Weeks	5	1246.89	249.4	4.58	2.29	3.17
Temp. x Weeks	7	810.06	115.7	2.12	2.08	(2.79)
Residual	131	7135.78	54.5			
Total	146	10952.86	75.0			

Height Gain - Whole experiment.

37) Variate = Total height gain.

Source of Variation	DF	SS	MS	VR	F 5%	F 1%
Provenance	6	980.39	163.40	61.25	2.10	2.82
Temperature	3	66.83	22.28	8.35	2.61	3.80
Weeks	5	63.07	12.61	4.73	2.22	3.04
Prov. x Temp.	18	61.15	3.40	1.27	(1.62)	(1.95)
Prov. x Weeks	30	96.25	3.21	1.20	(1.47)	(1.71)
Temp. x Weeks	7	78.72	11.25	4.22	2.02	2.66
Prov. x Temp. x Weeks	41	186.84	4.56	1.71	1.41	1.61
Residual	803	2142.21	2.67			
Total	913	3675.47	4.03			

Height Gain - Individual provenances.

38) Variate = 3028. Height gain.

Temperature	3	6.77	2.26	1.17	(2.68)	(3.94)
Weeks	5	6.07	1.21	0.63	(2.29)	(3.17)
Temp. x Weeks	7	29.11	4.16	2.15	2.08	(2.79)
Residual	122	236.22	1.94			
Total	137	278.17	2.03			

39) Variate = 3032. Height gain.

Temperature	3	13.62	4.54	1.37	(2.68)	(3.94)
Weeks	5	12.07	2.41	0.73	(2.29)	(3.17)
Temp. x Weeks	7	40.18	5.74	1.74	(2.08)	(2.79)
Residual	128	423.32	3.31			
Total	143	489.18	3.42			

40) Variate = 3053. Height gain.

Source of Variation	DF	SS	MS	VR	F 5%	F 1%
Temperature	3	23.67	7.89	2.48	(2.68)	(3.94)
Weeks	5	39.99	7.99	2.51	2.29	(3.17)
Temp. x Weeks	7	76.06	10.87	3.42	2.08	2.79
Residual	117	372.19	3.18			
Total	132	511.91	3.88			

41) Variate = 3059. Height gain.

Temperature	3	26.04	8.68	3.66	2.68	(3.94)
Weeks	5	29.21	5.84	2.46	2.29	(3.17)
Temp. x Weeks	7	21.61	3.09	1.30	(2.08)	(2.79)
Residual	124	294.02	2.37			
Total	139	370.89	2.67			

42) Variate = 3064. Height gain.

Temperature	3	24.01	8.00	3.57	2.68	(3.94)
Weeks	5	15.75	3.15	1.40	(2.29)	(3.17)
Temp. x Weeks	7	59.71	8.53	3.80	2.08	2.79
Residual	126	282.83	2.25			
Total	141	382.30	2.71			

43) Variate = 3004. Height gain.

Temperature	3	14.91	4.97	1.14	(2.77)	(4.15)
Weeks	5	24.93	4.99	1.14	(2.38)	(3.36)
Temp. x Weeks	6	31.81	5.30	1.21	(2.26)	(3.14)
Residual	57	248.83	4.36			
Total	71	320.48	4.51			

44) Variate = 3011. Height gain.

Source of Variation	DF	SS	MS	VR	F 5%	F 1%
Temperature	3	17.77	5.92	2.69	2.68	(3.94)
Weeks	5	28.81	5.76	2.61	2.29	(3.17)
Temp.x Weeks	7	11.57	1.65	0.75	(2.08)	(2.79)
Residual	129	284.57	2.21			
Total	144	342.72	2.38			

45) Variate = Clone 8000. Height gain.

Temperature	3	183.56	61.19	3.75	2.68	(3.94)
Weeks	5	155.88	31.18	1.91	(2.29)	(3.17)
Temp. x Weeks	7	482.08	68.87	4.22	2.08	2.79
Residual	129	2105.88	16.32			
Total	144	2927.41	20.33			

Branch Length - Whole Experiment.

46) Variate = Branch length.

Provenance	6	249.62	41.60	31.91	2.10	2.82
Temperature	3	33.12	11.04	8.47	2.61	3.80
Weeks	5	39.64	7.93	6.08	2.22	3.04
Prov. x Temp.	18	35.61	1.98	1.52	(1.62)	(1.95)
Prov. x Weeks	30	44.63	1.49	1.14	(1.47)	(1.71)
Temp. x Weeks	7	60.56	8.65	6.64	2.02	2.66
Prov. x Temp x Weeks	41	114.81	2.80	2.15	1.41	1.61
Residual	831	1083.58	1.30			
Total	941	1661.56	1.77			

Branch Length - Individual provenances.

47) Variate = 3028. Branch length.

Source of Variation	DF	SS	MS	VR	F 5%	F 1%
Temperature	3	11.49	3.83	3.15	2.68	(3.94)
Weeks	5	4.99	1.00	0.82	(2.29)	(3.17)
Temp. x Weeks	7	15.85	2.26	1.86	(2.08)	(2.79)
Residual	125	151.82	1.22			
Total	140	184.15	1.32			

48) Variate = 3032. Branch length.

Temperature	3	12.97	4.32	3.35	2.68	(3.94)
Weeks	5	5.52	1.10	0.86	(2.29)	(3.17)
Temp. x Weeks	7	19.07	2.72	2.11	2.08	(2.79)
Residual	131	168.78	1.29			
Total	146	206.33	1.41			

49) Variate = 3053. Branch length.

Temperature	3	4.11	1.37	0.92	(2.68)	(3.94)
Weeks	5	19.75	3.95	2.65	2.29	(3.17)
Temp. x Weeks	7	53.34	7.62	5.11	2.08	2.79
Residual	121	180.44	1.49			
Total	136	257.63	1.89			

50) Variate = 3059. Branch length.

Temperature	3	12.13	4.04	3.19	2.68	(3.94)
Weeks	5	26.12	5.22	4.12	2.29	3.17
Temp. x Weeks	7	21.01	3.00	2.37	2.08	(2.79)
Residual	131	166.03	1.27			
Total	146	225.29	1.54			

51) Variate = 3064. Branch length.

Source of Variation	DF	SS	MS	VR	F 5%	F 1%
Temperature	3	14.78	4.93	3.80	2.68	(3.94)
Weeks	5	7.83	1.57	1.21	(2.29)	(3.17)
Temp. x Weeks	7	43.28	6.18	4.77	2.08	2.79
Residual	132	171.05	1.30			
Total	147	236.93	1.61			

52) Variate = 3004. Branch length.

Temperature	3	4.51	1.50	1.08	(2.77)	(4.15)
Weeks	5	5.24	1.05	0.75	(2.38)	(3.36)
Temp. x Weeks	6	13.46	2.24	1.61.	(2.26)	(3.14)
Residual	58	80.60	1.39			
Total	72	103.81	1.44			

53) Variate = 3011. Branch length.

Temperature	3	8.68	2.89	2.34	(2.68)	(3.94)
Weeks	5	13.03	2.61	2.11	(2.29)	(3.17)
Temp. x Weeks	7	13.55	1.94	1.56	(2.08)	(2.79)
Residual	133	164.61	1.24			
Total	148	199.86	1.35			

54) Variate = Clone 8000. Branch length.

Temperature	3	213.48	71.16	12.26	2.68	3.94
Weeks	5	49.55	9.91	1.71	(2.29)	(3.17)
Temp. x Weeks	7	156.97	22.43	3.86	2.08	2.79
Residual	129	748.72	5.80			
Total	144	1168.71	8.12			

APPENDIX 7 Published paper:

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The influence of temperature on the cessation of height growth of Sitka spruce (Picea sitchensis (Bong.) Carr.) provenances

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Introduction

Sitka spruce is a native of West North America occurring in a narrow coastal belt from Kodiak Island and the Kenai Peninsula (61° N) to Mendocino County, California (39° N). Although of major importance in British forestry this species has been only recently the subject of physiological research.

The common occurrence of photoperiodic ecotypes in Northern Hemisphere tree species with a large north-south range was demonstrated by Sylven (1940) and was confirmed in *Picea* by Vaartaja (1959).

The decrease in daylength after mid summer is an important factor in initiating seasonal rest periods in conifers (Downs and Borthwick, 1956). Using artificial photoperiods Vaartaja (1959) showed that the critical daylength, for extension growth cessation in Sitka spruce, was greater for a northern (60° N) source than four a southern (43° N) and that the endogenous growth pattern was entirely overruled by the effects of photoperiod. This interaction between latitude of seed origin and photoperiod substantiated the presence of ecotypes in this species.

Provenance trials of Sitka spruce in the field have confirmed the photoperiodic control of apical growth cessation (Lines and Mitchell, 1966). Northern provenances, when grown in Britain, cease growth while other environmental factors remain favourable. The time of bud formation in Sitka spruce is closely correlated with latitude of seed origin and, in a nursery and glasshouse study (Burley, 1966) extended over 120 days for year-old seedlings of 47 provenances.

The regulation of the seasonal growth cycle of Sitka spruce has received less attention than other coniferous species in which continentality and altitude of seed origin have been shown to influence the photoperiodic response (Vaartaja, 1959; Irgens-Muller, 1957).

Growth and dormancy in Norway spruce (*Picea abies* (L.) Karst.) has been more widely studied (Dormling *et al.*, 1968; Robak and Magnesen, 1970). Extension of daylength did not compensate for unfavourable temperatures in the growth of Norway spruce seedlings (Magnesen, 1969) and an abnormally short photoperiod reduced growth regardless of temperature. Heide (1974) found that temperatures between 12 and 24° C did not alter appreciably the critical daylength of various Norway spruce provenances but higher temperatures accelerated the short day response.

This paper reports an experiment on the interaction of temperature and photoperiod on the setting and maturation of buds in a range of provenances of Sitka spruce.

Methods

1-year old seedlings of the eight provenances, detailed in *Table 1*, were potted in April 1973 and 'plunged' out of doors until midsummer. At the time of maximum natural photoperiod (19.75h on 24 June 1973) the plants were allocated randomly to treatments and transferred to four growth rooms. The plants were arranged in eight randomised blocks with 15 seedlings per provenance in each treatment.

Table 1. — Provenances of Sitka spruce (I.U.F.R.O. Collection)

I.U.F.R.O. No.	Provenance Location	Latitude N	Elevation (m)
3022	Dyea, Alaska	59°50'	0
3032	Kitwanga, Skeena/Nass R.	55°17'	670
3050	Copper Creek, Moresby Is.	53°13'	80
3059	Fair Harbour, Vancouver Is.	50°05'	30
3064	Vedder, Chilliwack, B.C.	49°12'	30
3002	Port Angeles, Washington	48°15'	110
3013	Tillamook, N. Oregon	45°33'	90-120
3017	Gold Beach, Oregon	42°50'	30

Table 2. — Experimental treatments in controlled environment rooms

Temperature °C		Humidity %		Vapour pressure deficit (mb)	
Day	Night	Day	Night	Day	Night
20	11	91	96	2.0	0.5
16	9	89	96	2.0	0.5
12	7	86	95	2.0	0.5
8	5	82	82	1.9	1.9

The 4 temperature treatments and associated conditions *(Table 2)*, were selected to relate to those at the latitudes of origin and to the suggested optimal temperature for photosynthesis in Sitka spruce (Nielsen *et al.*, 1971). All temperature treatments received the same photoperiod which was progressively reduced from 19h, at the start of the experiment, by hourly decrements to 17h and then by 30 min. wk^{-1}. The daily illumination cycle was as follows: —

e.g. a 17h day 2.5h daylight bulbs
12h bright fluorescent light (14,000 lux at plants)
2.5h daylight bulbs
7h dark

Decrements were made in the bright period. The soil was maintained at field capacity by daily watering and additions of liquid fertilizer made twice weekly.

Height measurements and recordings of the condition of the terminal apices were made weekly. As there was considerable variation in weekly height increment within provenances, and in individual plants in successive weeks, it was desirable to have some objective criterion of growth cessation. Extension growth was considered to have ceased, when the difference between the sample means of successive measurements did not exceed 1.6 mm, which was the detection limit of any change in height (detection limit = 3 × standard deviation of repeated measurement).

Table 3. — Photoperiod at time of extension growth cessation (h)

Treatment / Provenance	8/5°	12/7°	16/9°	20/11°
3022	17	16	16	15.5
3032	-	16.5	15.5	15.5
3050	16	16	16	14.5
3059	16	16	16	15
3064	16	16	15	15
3002	16	16	14.5	14.5
3013	16.5	16	14	13.5
3017	16.5	16	12	12

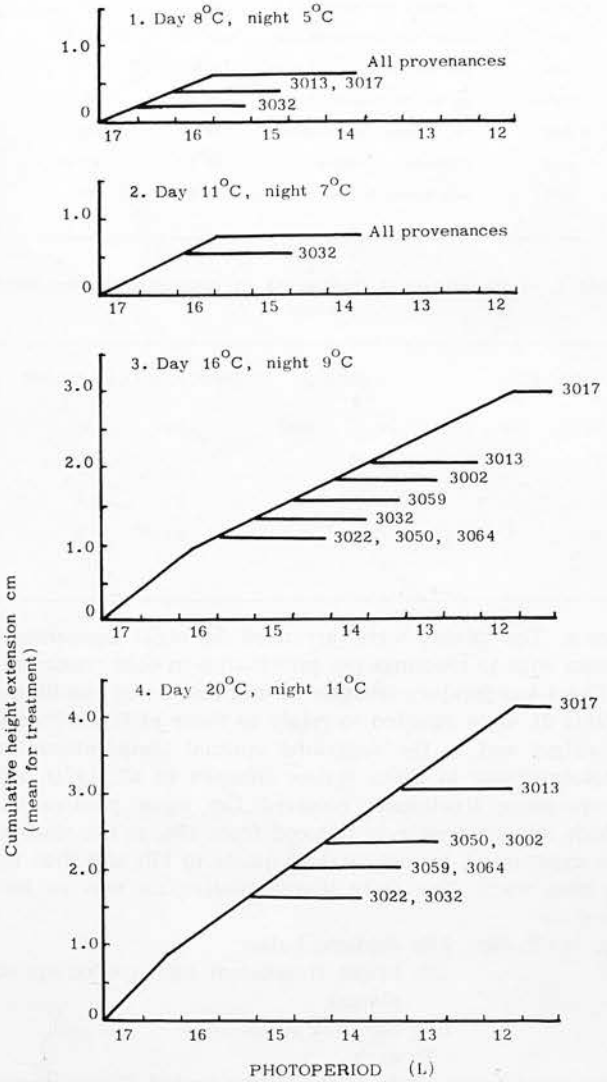

Figure 1. — Interaction of temperature and photoperiod on cessation of shoot extension of Sitka spruce provenances.

When extension growth had ceased in all provenances in all treatments the plants were removed from the growth rooms and wintered outdoors.

Results

The effect of the temperature treatments on the duration of extension growth and the photoperiod at its cessation are given in Table 3. The interaction of temperature and photoperiod on the rate of cumulative height growth and the order of its cessation in the different provenances is shown in *Figure 1*.

At the two cooler temperature regimes (8/5° C, 12/7° C), all provenances ceased height growth when the photoperiod reached 16h, whereas growth of southern provenances continued until the photoperiod was reduced to 12h in the warmer regimes (16/9° C, 20/11° C).

Shoot extension, in the two most northerly provenances, ceased at a photoperiod of 15.5h in all temperature treatments. The southern provenances displayed a wider range of temperature effects with the cooler regimes resulting in cessation of height growth at the relatively long daylength of 16.5h.

Differences in rate of shoot extension were noted for each provenance in the four temperature treatments. This, coupled with the differences in time of growth cessation, accounts for the large variation in height attained between treatments. Although the limit of detection of height increment provided a useful criterion of growth cessation for each provenance sample, many plants continued to make additional extensions during the remainder of the experiment. These additional increments are shown in *Table 4*. The 20/11° C treatment resulted in the greatest height increments due to greater growth rates and, particularly, longer periods of growth.

To take the variation in successive height increments of individual plants into account an analysis of variance was performed in which the cessation of growth for each plant was assumed to occur when its weekly increment first fell below 1.6 mm.

Source of variation	DF	SS	MS	VR
Provenance	7	102.3	14.6	5.0
Temperature	3	685.4	228.5	79.0
Interaction	20	484.9	24.2	8.4
Residual	387	1119.1	2.9	
Total	417	2391.8	5.7	

All the variance ratios are highly significant ($p \leqslant 0.01$) but the overriding influence of the temperature treatments on the time of cessation is clear.

The mean duration of growth in weeks after the summer solstice, based on individual plants, is given by provenance and temperature treatment in *Table 5*. The provenances show a latitudinal trend in termination of extension growth comparable with the field results of Lines and Mitchell (1966), while the duration of growth doubles between the coolest and warmest treatments.

Table 4. — Mean height growth of provenances (cm)

Treatment	8/5°		12/7°		16/9°		20/11°	
Provenance	a	b	a	b	a	b	a	b
3022	0.6	0.9	1.2	1.6	1.8	1.9	2.4	2.5
3032	0.0	0.3	0.5	0.8	1.8	2.0	1.9	2.0
3050	1.3	1.5	1.2	1.7	1.7	2.4	2.7	2.8
3059	1.2	1.4	1.7	2.3	2.3	2.6	3.1	3.4
3064	1.1	1.4	1.2	1.9	1.6	2.2	2.6	2.8
3002	1.0	1.2	1.4	1.9	2.5	2.7	3.2	3.3
3013	0.7	1.2	1.5	2.2	2.4	2.6	3.7	3.9
3017	0.8	1.2	1.4	2.3	3.0	3.0	4.8	4.8

a) when weekly extension no longer detectable.

Table 5. — Mean duration of height growth (weeks) for individual plants

Treatment / Provenance	8/5°	12/7°	16/9°	20/11°	Overall Mean
3022	3.38	5.50	4.86	5.83	4.89
3032	3.02	4.39	5.61	5.18	4.55
3050	5.00	5.20	6.07	6.20	5.62
3059	4.67	5.20	6.53	6.40	5.02
3064	4.13	4.14	5.27	6.53	5.70
3002	4.20	5.46	5.67	7.60	5.73
3013	3.54	4.79	5.73	8.47	5.63
3017	2.51	4.67	4.58	12.25	6.00
Overall Mean	3.84	4.93	5.56	7.18	

Bud development was enhanced by the higher temperatures; terminal buds becoming visible 1—3 weeks after height growth ceased in the 20/11° C treatment and 2—6 weeks later in the 16/9° C treatment. In the two cooler treatments buds could only be detected visually 8—9 weeks after cessation of growth.

The influence of the different temperature regimes during bud maturation on flushing in the spring of 1974 was recorded in the open. Breaking of bud dormancy followed a latitudinal trend from northern to southern provenances, while the northern provenances subjected to the cooler bud maturation temperatures (also the longest periods after bud development) flushed first. Southern provenances flushed up to 1 month later and displayed greater variation between treatments.

Discussion and Conclusions

Bud formation in Norway spruce tends to occur slightly earlier in nursery than in glasshouse grown plants and Dormling (1973) attributes this to a temperature effect once a critical night length has made the plants receptive to lower temperatures. In Magnesen's (1971) experiments some Norway spruce of southerly provenances (Ca. 48° N) showed no response to short periods of lowered night temperatures until late summer, when bud formation was enhanced. In the experiment reported here, although the temperature regimes were constant and did not include night temperatures below 5° C, they had marked effects on the photoperiod at which apical shoot growth ceased. As the experiment began at midsummer, it is unlikely that any photoperiodic conditioning could have taken place yet the lower temperature regimes resulted in no further shoot extension after the photoperiod had reached 16h. An exception might be the Kitwanga provenance (3032) from a high elevation (670 m) at latitude 55° N in an area of introgression with white spruce *(P. glauca* (Moench.) Voss.). At the start of the experiment a high proportion of these plants had already formed buds by the longest photoperiod of 19.75h in the Edinburgh area (56° N), indicating an adaptation to a short warm season. A similar instance for a Norway spruce provenance from latitude 64° N is discussed by Heide (1974).

The plants used in this experiment were lifted from the same bed of a nursery provenance trial and potted before flushing in their second year. They thus had buds which would be extended into shoots of a predetermined length after flushing in early May and the experiment was designed to start before extension growth would normally be expected to cease. Growth continuing beyond that predetermined in the bud has been termed 'free' and shown to occur in the early years of several species and has recently been demonstrated for 4-year old Black spruce *(Picea mariana* (Mill) B.S.P.) provenances in Canada (Pollard and Logan 1974). These authors further demonstrated (1975) that 'free' growth could be induced in the second growth cycle of Black spruce by a high temperature treatment (25° C) at photoperiods in excess of 12h. It seems probable that the Sitka spruce provenances in this experiment at the higher temperatures were in 'free' growth.

This is supported by a comparison of duration of growth between these 2-year seedlings and two vegetatively propagated clones of older Sitka spruce included in the experiment. Neither clone, of probable Queen Charlotte Island provenance, grew for more than 3—4 weeks in any treatment indicating that they had little or no capacity for free growth in these conditions.

From *Table 3* it appears that the highest temperature had the greatest effect on duration of growth and that it was related inversely to latitude of origin. Conversely the southern provenances seem to be more sensitive to low temperatures *(Table 5)* than those origins from the middle of the range. These results support Pollard and Logan's contention that 'free' growth is environmentally controlled.

In general the results show that photoperiod does not control cessation of apical shoot extension in Sitka spruce absolutely but that higher temperatures may be important in shortening the critical daylength while low temperature appears to upset the commonly accepted latitudinal relationship between photoperiod and growth cessation.

Bud development to the stage where it becomes visible is clearly affected by the ruling temperature regime and the results with Sitka spruce are similar to those published by Magnesen (1969) for Norway spruce. At low temperatures the process of development is slower.

Flushing, in the spring following the experiment, followed the general pattern, described by Burley (1966), of northern provenances first with greater variation in the southerly provenances. This makes it difficult to assign any effects to the experimental treatments although it appeared that low temperatures advanced flushing dates.

Of necessity controlled environment experiments are conducted on newly germinated seedlings, or as in this case, young transplants which are still capable of free growth in suitable conditions. Older trees tend to have predetermined annual growth and this age effect and the relationship between meristems responsible for shoot extension, leaf initial formation and cambial activity require further investigation before results of controlled environment experiments can be extrapolated to field conditions.

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Summary

The observed time of bud formation in Sitka spruce is closely linked with the latitude of seed origin and shows a north-south progression. The effect of 4 different temperature regimes on cessation of apical shoot extension has been investigated in controlled environments.

Eight provenances covering the latitudinal range of the species were transferred to growth rooms, at mid summer

1973, where day/night temperatures were 20/11° C, 16/9° C, 12/7° C and 8/5° C respectively. Photoperiods were reduced progressively at 0.5h wk^{-1} while weekly height measurements were made to determine growth cessation.

At the cooler temperatures shoot extension in all provenances ceased at 16h, whereas the higher temperatures allowed growth in southern provenances to continue until a 12h photoperiod was reached. The northern-most provenances ceased growth at 15.5h in all treatments. It was concluded that the critical photoperiods for shoot extension could be markedly affected by temperature in southern provenances but less so in those from the north. Bud development was delayed by low temperature but this appeared to advance flushing dates in the following year.

Key words: Provenance, Sitka spruce, growth cessation, temperature, photoperiod.

Zusammenfassung

Im Jahre 1973 wurden in Schottland 1jährige Sämlinge von *Picea sitchensis* (Bong.) Carr. aus 8 Provenienzen, von Oregon bis Alaska = 42° 50' bis 59° 50' nördlicher Breite und 0 bis 670 m Seehöhe, auf die Beendigung des Triebwachstums während der Vegetationsperiode untersucht. Die Behandlung erfolgte in Klimaräumen unter vier verschiedenen Tag/Nacht Temperaturbedingungen ab 24. Juni. Die Belichtungsdauer wurde danach fortschreitend um 30 Min. wöchentlich gesenkt.

Die nördlichen Provenienzen stellten in allen Behandlungsarten das Triebwachstum ab einer Tageslänge unter 15,5 Stunden ein, während die südlichen Provenienzen bei genügend hoher Temperatur das Wachstum bis herunter zu 12 Stunden fortsetzten.

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